Uno de los hitos más importantes de la Ecología de Poblaciones es entender cómo las poblaciones varían sus parámetros demográficos respondiendo a cambios ambientales. Es este un tema cada vez más importante debido a los cambios globales que están afectando el planeta. En ente contexto son de particular interés los procesos de dispersión, de colonización, de crecimiento poblacional y de cómo éste se ve afectado por diversos parámetros demográficos de poblaciones estructuradas (e.g. por clases de edad, sexo y estado reproductor). Disponer de datos adecuados para investigar estos procesos no es tarea fácil puesto que se requiere de un seguimiento a largo plazo que en especie longevas como es el morito, se traduce en muchos años de recolección de datos. Además de esto, una dificultad añadida para este tipo de investigación es disponer de datos que hayan sido recolectados desde la formación de una población. No obstante, de no disponer de esta información no es posible investigar los aspectos quizás más relevantes de estos procesos.

Este estudio ha sido posible gracias al esfuerzo y dedicación de personal investigador y técnico (Equipo de Seguimiento de Procesos Naturales) de la Estación Biológica de Doñana, a su capacidad de previsión que les ha llevado a seguir la población de morito en Doñana desde su aparición con tan sólo siete parejas reproductoras, y finalmente gracias a la participación de muchos voluntarios. Los objetivos de esta tesis han sido describir y analizar la dinámica poblacional de esta especie modelo con el fin de investigar cuáles son los factores más influyentes en el proceso de colonización, crecimiento y expansión de una especie.

Dinámica y dispersión de una especie en expansión, el morito (Plegadis falcinellus)
TESIS DOCTORAL 2014
Simone Santoro

Dinámica y dispersión de una especie en expansión, el morito (*Plegadis falcinellus*)

TESIS DOCTORAL 2014

Simone Santoro

Estación Biológica Doñana CSIC

Universidad de Sevilla

Dinámica y dispersión de una especie en expansión, el morito (*Plegadis falcinellus*)

Memoria presentada para optar al Grado de Doctor en Biología por la Universidad de Sevilla por el Licenciado

Simone Santoro

Sevilla Diciembre 2014

Director
Dr. Jordi Figuerola Borras
Investigador
Departamento de Ecología de Humedales
Estación Biológica de Doñana
Sevilla - España

Director
Dr. Andy J. Green
Investigador
Departamento de Ecología de Humedales
Estación Biológica de Doñana
Sevilla - España

Tutor
Dr. Laura Serrano Martín
Profesora e investigadora
Departamento de Biología Vegetal y Ecología
Universidad de Sevilla
Sevilla - España

Tabla de Contenidos

Introducción general

El marco teórico

La Ecología se puede entender como el estudio de las dinámicas de los organismos vivientes y de cómo estos procesos interaccionan con el ambiente que les rodea. No sin motivo, uno de los autores modernos más influyentes en ecología, Charles J. Krebs, titula su obra [1] "The Experimental Analysis of Distribution and Abundance". A menudo se considera que el conjunto de los seres vivos se organiza según una estructura jerárquica que incluye diferentes escalas, diferentes niveles de organización [2]. Al margen del nivel considerado (individuos, poblaciones, metapoblaciones, etc.), sus dinámicas pueden describirse por parámetros demográficos del todo análogos entre las diversas escalas de interés y cuantificables a través de herramientas de análisis demográficos [3]. En particular, la Ecología de poblaciones se ocupa de entender cómo el número de individuos en las poblaciones así como su distribución en el espacio se regula por parámetros demográficos como son la productividad, mortalidad, reclutamiento, inmigración y dispersión.

Razón de sexos y su importancia para la Ecología de poblaciones

Otro parámetro importante para el crecimiento poblacional es la proporción de sexos. El numero de individuos en una población es un parámetro relevante al estudiar, por ejemplo, la competencia entre los individuos o la regulación de la población por los recursos existentes (véase [4] para un ejemplo con la especie de estudio de esta tesis doctoral). Sin embargo, al estudiar el crecimiento de una población es el número de hembras reproductoras el parámetro mas relevante puesto que de ello depende cuantos nuevos individuos van a nacer. Por este motivo variaciones en la proporción de sexos pueden tener efectos muy importantes sobre las dinámicas poblacionales [5]. El estudio de los factores evolutivos que afectan a la proporción de sexos dio lugar a la teoría de la asignación por sexo

(*sex allocation theory*) [6] desarrollándose en uno de los campos de investigación más activos en la Ecología evolutiva [7]. Como se ha mencionado anteriormente, la proporción de sexos es una variable fundamental para describir la pirámide poblacional que además de definir su estado demográfico representa un eslabón importante para el estudio de su dinámica [8]. En otras palabras, la razón de sexos de diversas clases de edad o estado reproductor puede afectar directamente los procesos de denso-dependencia que regulan la dinámica de una población. Esto ocurre porque las hembras determinan la abundancia de la progenie, y resulta entonces útil y necesario conocer la proporción de sexos para conocer el efecto de la densidad poblacional sobre su productividad. El estudio de la proporción de sexos representa así un importante, pero algo infravalorado, puente conceptual entre dos disciplinas que tantos puntos de contactos mantienen entre ellas: la Ecología evolutiva y la Ecología de poblaciones. Por ejemplo, las poblaciones de vertebrados suelen ser caracterizadas por una mayor complejidad frente a las especies modelo sobre las que se han teorizado los modelos de asignación por sexo y, por ejemplo, las generaciones suelen sobreponerse entre ellas en una misma población. Es entonces posible que las razones de sexos de diversas clases de edad puedan afectarse las unas a las otras a través de cambios en parámetros demográficos específicos por sexo y clase de edad cuyo fin es optimizar la eficacia biológica de la población. No obstante, un número muy limitado de estudios ha considerado estas cuestiones a la hora de investigar patrones de razón de sexos en poblaciones de vertebrados (véase [7] para una discusión detallada sobre este tema).

Estrategia vital

La estrategia vital (*life-history*) de una especie, es decir el conjunto de eventos determinantes en su ciclo de vida se describe a

través de parámetros demográficos que forman parte integrante de lo que la Ecología de poblaciones se propone investigar [9]. Así que la estima de la fecundidad, razón de sexos, supervivencia, edad de primera reproducción, longevidad y dispersión han sido y siguen siendo el objetivo primario de un gran número de modelos demográficos que usan diversos tipos de datos siendo los datos de captura-recaptura y de censos los más empleados [10,11]. Conocer la estrategia vital de una especie también es fundamental para la Biología de la Conservación en cuanto permite diseñar políticas de gestión eficaces difíciles de alcanzar sin este conocimiento [12]. Asimismo, los caracteres de la estrategia vital (*life-history traits*) tienen mucho interés del punto de vista evolutivo puesto que son modelados por la selección y en su conjunto determinan la eficacia biológica (*fitness*) de un individuo [9,13]. Por esta razón, poder cuantificar estos parámetros a menudo es de mayor interés para contrastar teorías ecológico-evolutivas con datos empíricos [14].

Dispersión

Otro aspecto crucial en la estrategia vital de una especie es la capacidad que sus especimenes tienen de dispersar. Este proceso y los factores intrínsecos y extrínsecos que lo regulan afectan al flujo génico entre poblaciones, el número de individuos que las componen así como su distribución dentro de la metapoblación [15,16]. La dispersión, al contrario que la migración, no es necesariamente estacional y es heterogénea entre diversos individuos de una misma población [17]. Este proceso proporciona una respuesta rápida a alteraciones de diverso tipo y magnitud como pueden ser cambios climáticos abruptos o modificaciones inesperadas de la matriz ambiental. Existen diversos tipos de dispersión aunque también existe cierta falta de acuerdo entre los ecólogos sobre su clasificación [15]. Posiblemente la principal subdivisión que suele hacerse es entre la dispersión natal y la dispersión reproductora. En el primer caso se

trata del movimiento que un individuo hace para abandonar su sitio de nacimiento hacia un nuevo sitio donde recluta como reproductor; en el segundo, a un movimiento para cambiar de sitio de reproducción. Algunos autores también se refieren a la dispersión invernal como a aquel movimiento que un individuo hace al cambiar de sitio de invernada. También se suelen considerar tres fases durante el proceso dispersante: 1) la salida, 2) el viaje y 3) la llegada. Cada una de estas fases puede ser afectada por diversas causas y costes asociados: es de este conjunto de factores que depende el evento de dispersión [18,19]. Así que es de esperar que sean las condiciones ambientales e individuales en el sitio de partida que más afectarán la probabilidad que un individuo disperse o no, pero son las condiciones de la matriz ambiental que el dispersante atraviesa así como del sitio de llegada las que finalmente determinan dónde y si un individuo es capaz de dispersar. Por esto es importante para la conservación no sólo gestionar adecuadamente aquellas áreas que ya están siendo utilizadas por una especie o por un conjunto de ellas, sino también preservar la conectividad entre éstas y la existencia de otras que aun no ocupadas en la actualidad podrían serlo en futuro [16].

Cambio global

En el contexto actual de cambio global comprender los factores que regulan la dispersión de los individuos y sus consecuencias poblacionales es de interés especial debido a su estricta relación con el flujo génico y la distribución y persistencia de las poblaciones [15]. Ya son apreciables importantes cambios en la distribución de las especie como resultado del cambio global y se espera que este proceso se intensifique en el futuro próximo [20]. Existen diversos mecanismos que establecen esta relación entre el cambio global y la distribución y persistencia de las especies: (*i*) afectando la fenología de las especies así como las condiciones del nicho ecológicos en el

que viven, (*ii*) modificando y fragmentando los hábitats o (*iii*) alterando las respuestas fisiológicas de los individuos a través de los cambios ambientales [21–23]. Como patrón general las especies de aves parecen estar ampliando y desplazando sus áreas de distribución hacia los polos [24], pero se necesitan mas estudios sobre el tema puesto que también se ha observado el patrón contrario con especies que están disminuyendo su área de distribución aparentemente como consecuencia directa o indirecta del cambio climático [21,25]. Alrededor de un 35% de las especies de aves tienen rasgos que las hacen particularmente susceptibles al impacto del cambio climático [26]. Los eventos climáticos extremos (sequías, tifones, etc.) son los que mayor repercusión tienen sobre la dinámica poblacional de muchas especies de aves [25,27]. Por esta razón es crucial para diseñar políticas de gestión adecuadas investigar los efectos que el cambio global puede estar teniendo sobre los parámetros vitales y la distribución de las aves así como de otros taxa. Pero para ello se requieren estudios basados en los cada vez más escasos programas de monitoreo y recogida de datos a largo plazo. Mientras existe un número limitado de estudios que han puesto en relación la supervivencia con patrones climáticos (por ej. eventos climáticos extremos), casi no existen estudios que hayan investigado estos efectos sobre la dispersión o el reclutamiento [25].

Crecimiento poblacional: auto-reclutamiento, inmigración y emigración

Una serie de caracteres de la estrategia vital cuantificables como parámetros demográficos (supervivencia, productividad, edad de primera reproducción, razón de sexos) determinan el crecimiento poblacional. Entre estos, una fuerte dicotomía existe entre el reclutamiento de individuos reproductores a partir de la propia población o de otras, o sea entre auto-reclutamiento e inmigración. La importancia de esta dicotomía se debe a que, en el contexto

metapoblacional [28], se trata de procesos demográficos cruciales para la conectividad entre poblaciones. De manera que la contribución del uno y del otro para el crecimiento poblacional tiene mucho que ver con la dinámica fuente-sumidero (*source-sink* en inglés; [29]) que tanta relevancia tiene en el funcionamiento de una metapoblación [30]. Por definición, una población sumidero (*sink*) en el caso de no recibir inmigrantes es destinada a extinguirse mientras que una población fuente (*source*) es una población con una tendencia a mantenerse numéricamente estable o al alza y con un cierto número de individuos dispersando hacia otras poblaciones. Aunque la inmigración y el auto-reclutamiento sean procesos fundamentales para la dinámica poblacional de una especie, existen dificultades metodológicas que han limitado su estudio. Ha sido sólo en los últimos años cuando un contexto metodológico adecuado ha permitido estimar tasas de dispersión entre poblaciones y validar estadísticamente diferentes hipótesis sobre los factores ecológicos que afectan este proceso ([31,32] para otros aproches). Estos estudios suelen necesitar datos de seguimiento de las diversas poblaciones que componen una metapoblación, algo que, como no es de extrañar, resulta muy difícil de lograr en la práctica ([30,33]; pero véase [34]).

Inmigración, auto-reclutamiento y crecimiento poblacional son procesos potencialmente implicados en la formación y crecimiento de nuevas poblaciones. Los estudios realizados hasta el momento se han centrado principalmente en colonias de aves marinas, concluyendo que durante los primeros años después del establecimiento de una nueva colonia su crecimiento se debe mayoritariamente a la inmigración ([32,35–37]; aunque véase [38]). Así que un rápido crecimiento poblacional puede ocurrir también cuando un número muy exiguo de individuos se asientan para formar una nueva colonia debido a la atracción de otros individuos. Existen diversas hipótesis sobre cuáles son los factores que influyen sobre el reclutamiento

(local y por inmigración), como son la disponibilidad de recursos tróficos, la competición intra e inter-específica y el éxito reproductor de la colonia ([39] para una revisión sobre aves). En particular la calidad reproductora de una colonia, señalada por la mera presencia de conspecíficos [40–42] o por su éxito reproductor [43,44], parece jugar un papel particularmente importante para el reclutamiento de individuos. Por lo tanto no es de extrañar que, como se ha demostrado para una colonia de charranes comunes (*Sterna hirundo*; [45]), la tasa de inmigración puede tener una fuerte relación positiva con la abundancia de reclutas locales. Esto sugiere entonces que auto-reclutamiento e inmigración pueden formar parte de un mismo proceso que se retro-alimenta creando e impulsando el crecimiento hasta que factores de denso-dependencia entran en juego. No obstante la relevancia que estos temas tienen en Ecología de poblaciones, existe una escasez de estudios que hayan investigado estos patrones en poblaciones de reciente formación y la mayoría de ellas se han llevado a cabo con aves marinas. Por tanto, para poder generalizar los resultados obtenidos hasta el momento, se hace patente la necesidad de otros estudios con especies que tengan estrategias vitales diferentes.

Efectos de la densidad poblacional

La denso-dependencia, la relación causal entre el tamaño poblacional y los parámetros demográficos, tiene un papel central en las dinámica de la poblaciones. Estudios clásicos de denso-dependencia se han centrado en la relación entre tamaño poblacional y éxito reproductor en especies coloniales [46]. Más recientemente se ha puesto el foco de estos estudios sobre el conjunto de parámetros demográficos puesto que es de esperar que de existir un efecto, éste se refleje en la eficacia biológica de un individuo que depende de todos estos parámetros. Así por ejemplo Serrano et al. [47] han usados modelos de captura-recaptura para estudiar como el tamaño

de diversas colonias de cernícalo vulgar (*Falco naumanni*) se relacionaba a la supervivencia y a la dispersión además que a la probabilidad de depredación del nido. Sus resultados indican que para colonias más grandes la mortalidad, la dispersión y el peligro que sus nidos sean depredados es menor que en colonias más pequeñas sugiriendo así un claro efecto Allee, o sea una respuesta positiva en términos de eficacia biológica al aumentar la densidad poblacional. Este tipo de relación puede deberse a varios mecanismos como una mayor protección contra los depredadores y en general a una forma más eficaz de explotar los recursos disponibles, o una mayor heterogeneidad genética de la población debido a un menor grado de endogamia, o también a una mayor resistencia a eventos estocásticos de fluctuación poblacional [48]. No obstante, la densidad poblacional puede influir negativamente sobre el ciclo vital de los individuos a través de varios mecanismos como por ejemplo: disminuir la cantidad de recursos disponibles per capita, aumentar el riesgo de difusión de patógenos, incrementar el uso de sitios de mala calidad, aumentar la proporción de juveniles en la pirámide poblacional y a su vez el éxito reproductor medio de la población.

Es de esperar que el efecto de la densidad sea negativo para las territoriales y positivo para las coloniales [49]. Esto desde luego representa una simplificación extrema de cómo este proceso puede variar según algunas características de las diferentes especies: en la realidad entran en juego muchos otros factores siendo uno de estos el mismo tamaño poblacional. De hecho los efectos de la densidad sobre la eficacia biológica pueden variar drásticamente en función del tamaño poblacional, aumentando para poblaciones más cercanas a la capacidad de carga [50].

El sistema-modelo

El morito es una especie que estuvo presente en tiempos históricos en Doñana y en otras regiones de la península ibérica pero

que tan sólo volvió a establecerse como reproductor a finales del siglo pasado. Las primeras parejas se establecieron en la costa valenciana (1993), luego en el Delta del Ebro y en Doñana (1996) [51]. Mientras las poblaciones de la costa oriental española tuvieron un crecimiento limitado en el tiempo e incluso algunas desaparecieron a los pocos años, la población de Doñana tuvo un crecimiento impresionante desde las siete parejas que se establecieron en 1996 en el Lucio de la FAO, alcanzando más de 8000 parejas en los últimos años (Manuel Mañez, comunicación personal). El Lucio de la FAO es un espacio protegido y restaurado con un regimen semi-artificial de bombeo de agua que alberga un centro visitantes del Parque. A partir de esta colonia y después de un rápido crecimiento poblacional se establecieron nuevas colonias de cría especialmente en el Espacio Natural Doñana. Este acontecimiento fue acompañado desde sus comienzos por una intensa actividad de monitoreo de esta población, realizado por el Equipo de Seguimiento de Procesos naturales de la Estación Biológica de Doñana (EBD) y por personal investigador de este centro. En cada estación reproductora se marcaron con anillas metálicas y de lectura a distancia (PVC alfanuméricas), se censaron las colonias en cuanto a número de parejas reproductoras, nidos, pollos volantones además de otras actividades de observación del estado de la colonia [52]. También se realizaron lecturas a distancia de individuos marcados en el Espacio Natural Doñana en diversos periodos del año. Además del impresionante y rápido aumento poblacional local, esta especie también ha tenido una rápida expansión en la Cuenca del Mediterráneo y en Europa Occidental siendo la población reproductora e invernante de Doñana la más relevante en términos numéricos. Debido a todo lo anterior, los datos procedentes del monitoreo exhaustivo de esta especie proporcionan un sistema-modelo ideal para el estudio de la dinámica poblacional. En particular, es de especial interés el poder testar diversas hipótesis sobre la dinámica poblacional siendo ésta una especie en pleno

crecimiento, en un ambiente altamente imprevisible y que podría haber jugado un papel clave para la expansión de la especie.

La cuestión metodológica

El conocimiento de los procesos que regulan las poblaciones animales así como sus características ecológicas y evolutivas pasa por el estudio de sus parámetros demográficos también denominados caracteres de estrategia vital (*life-history traits*) [10]. Entre las herramientas de análisis que más se han usado y se usan para estimar parámetros demográficos y testar diversas hipótesis sobre sus dinámicas encontramos en primer lugar los métodos de captura-recaptura. El origen de estos métodos se remonta entre el siglo XIX y el XX teniendo como objetivo la estima de un parámetro específico: la abundancia [53,54]. El fundamento base de todos estos métodos, inclusive los más modernos, es la estima de la probabilidad que los individuos marcados tienen de ser detectados (captura, avistamiento, recuperación, muestra de genética, etc.) a partir de las cuales se puede estimar el parámetro de interés biológico. Un primer avance importante nació de la constatación que las poblaciones naturales rara vez son cerradas demográfica (no nacimientos/muertes) y geográficamente (no entradas/salidas de individuos) sino que los parámetros que las caracterizan son dinámicos y responden a variaciones ambientales y/o demográficas. Esto hizo necesario centrar el foco de la investigación en la estima de las tasas vitales (i.e. supervivencia, dispersión, reclutamiento) que definen los cambios poblacionales y sobre los cuales es posible analizar diversas hipótesis ecológicas y evolutivas [10,55]. La captura-recaptura ha tenido un desarrollo impresionante en los últimos 20-30 años (véase [56] para un resumen detallado) en cuanto a cantidad de modelos, tipo de análisis, algoritmos para la estima de los parámetros y métodos de selección de los modelos; no resulta entonces posible dar

una visión global, aunque sintética, del conjunto de estas metodologías en la introducción de una tesis doctoral.

En cuanto al tipo de análisis de captura-recaptura usado a lo largo de esta tesis doctoral, han tenido particular interés los modelos multi-estado [31,57] y los modelos multi-eventos [58,59] que representan una generalización de los primeros. Los modelos multi-estado se usan para modelar datos de captura-recaptura que además de contener información sobre la captura u observación de un individuo marcado, también consideran el estado en el que el individuo se encuentra al ser capturado. Por "estado" se refiere uno a algún tipo de característica categórica que define el individuo capturado: sexo, sitio, clase de edad, estado reproductor, estado immunológico, etc. Por lo que se refiere a la dinámica poblacional, estos modelos resultan particularmente útiles para estimar las tasas de inmigración/emigración así como la supervivencia real en el ámbito de una metapoblación cuyas poblaciones hayan sido monitoreadas durante un periodo de tiempo y con un esfuerzo de recaptura suficientes. Una fuerte limitación de los modelos multi-estado suele ser la dificultad de registrar el estado del individuo en cada una de sus recapturas/observaciones. Por lo tanto, en esos casos una gran cantidad de información se pierde debido a que las recapturas sin el conocimiento del estado del individuo no se pueden incluir adecuadamente en los análisis. Los modelos multi-eventos permiten solucionar este tipo de limitaciones además de reducir la heterogeneidad en los datos teniendo en cuenta la incertidumbre sobre el estado de un individuo recapturado. En particular define el concepto de eventos como lo que uno realmente sabe. Por ejemplo, un individuo puede haberse capturado y su estado biológico (véase antes) desconocerse por completo o no ser del todo cierto: a esa recaptura con esa información (incierta) se le define "evento". La probabilidad que un evento ocurra se considera que depende

exclusivamente de los estados biológicos a los que se relacionan y cuyas transiciones entre ellos obedecen a una cadena de Markov.

Además de los modelos de captura-recaptura, las matrices de proyección poblacional representan otra herramienta muy útil para el estudio de las dinámica poblacionales y para inferencias de tipo predictivo sobre la tendencia de una población según diversos escenarios. Estos modelos, consideran que la población se estructura por clase de edades o por estados (sexos por ejemplo) cada uno con sus propios valores de supervivencia y de fecundidad [60]. Estas matrices, combinadas con valores de parámetros demográficos estimados por captura-recaptura y por estimas de fecundidad nos permiten estimar la tasa de crecimiento esperada si la dinámica dependiera únicamente de factores demográficos intrínsecos (sin inmigración/emigración o con una tasa neta de inmigración igual a cero). Existen muchos tipos de modelos matriciales, con aproximaciones muy distintas (por ejemplo determinística o estocástica) y con fines muy diferentes (véase [11,61]). En general estos modelos son usados (*i*) para una investigación retrospectiva de la dinámica poblacional, por ejemplo para estimar cuál habría sido el crecimiento esperado en un intervalo de tiempo pasado según un cierto conjunto de parámetros demográficos; o (*ii*) para hacer proyecciones de lo que sería la dinámica poblacional (por ejemplo el tamaño poblacional) dentro de un periodo de tiempo futuro según ciertos valores demográficos de partida. Así que mientras en el primer caso se puede estimar la contribución de la inmigración confrontando el crecimiento poblacional esperado según factores intrínsicos con el esperado [30,33,62], en el otro se pueden hacer predicciones sobre la persistencia o menos de una población de estudio [63]. El papel que estas herramientas pueden tener para diseñar políticas de gestión y conservación resulta particularmente claro cuando se simula el efecto de diversos escenarios demográficos sobre el crecimiento poblacional o se analiza la sensibilidad a cambios

de valores demográficos para identificar, por ejemplo, las clases de edad que mayor peso tienen sobre la dinámica poblacional (véase [64]).

Una característica común de los modelos matriciales es el uso de información de origen diverso (por ej. conteos, datos de captura-recaptura, estimas de fecundidad, etc.) para investigar las dinámica poblacionales. Este patrón general es cada vez más utilizado en Ecología (véase por ejemplo el uso de modelos integrados de dinámica poblacional; [65]) puesto que a menudo dificultades logísticas de cualquier tipo impiden tener datos exhaustivos de una sola fuente. Por ejemplo es muy común no disponer de datos de captura-recaptura a nivel metapoblacional sino tenerlos sólo para una o pocas poblaciones ([33], pero véase [34]). En estos casos resulta entonces imposible discriminar entre mortalidad y emigración permanente así como investigar el proceso de dispersión de la población. El uso de diversos tipos de datos y aproches metodológicos pueden en ciertos casos proporcionar una respuesta al menos parcial del problema que se pretende resolver.

Varias de estas aproximaciones metodológicas son las que han permitido abordar algunas de las cuestiones relevantes sobre la dinámica de poblaciones identificadas en esta Introducción.

Objetivos de la tesis doctoral

En esta tesis doctoral he usado datos de captura-recaptura (reavistamiento), control de la colonia y censos poblacionales para determinar la dinámica poblacional de una especie en expansión en el área del Mediterráneo y Europa occidental a partir de la población de Doñana. Dentro del marco conceptual definido anteriormente, he definido cuatro objetivos principales:

1. Describir el papel que la creación y gestión de un espacio semi-natural protegido (FAO) ha tenido sobre la dinámica poblacional de la especie-modelo de esta tesis doctoral y de otras especies de ardéidos que crían en la misma localidad.

2. Analizar los factores intrínsicos y extrínsecos que han modulado el proceso de dispersión del morito de Doñana permitiendo su expansión en el Mediterráneo y Europa Occidental. Siendo las condiciones ambientales en Doñana muy variables se ha analizado el efecto que los episodios de sequía local en época reproductora han tenido sobre el proceso de dispersión de esta población.

3. Determinar desviaciones de la proporción de sexos a nivel poblacional de las esperadas según (*i*) el proceso meiótico, (*ii*) el coste de cría esperado por el sexo de los pollos o (*iii*) en respuesta a la variación temporal de factores ambientales y/o demográficos.

4. Investigar el proceso demográfico que ha favorecido el crecimiento poblacional del morito en Doñana a partir de su asentamiento en la colonia de la FAO dependiendo de sus parámetros vitales: productividad, mortalidad, reclutamiento local e inmigración neta. Asimismo, se ha investigado su papel en las dinámicas poblacional para testar si su crecimiento ha sido determinante para la expansión de la especie (población fuente o sumidero).

Bibliografía

1. Krebs C (2009) Ecology: The Experimental Analysis of Distribution and Abundance. 6th editio. San Francisco, USA.
2. Begon M, Harper J, Townsend C (1986) Ecology: individuals, populations and communities. London, UK.: Blackwell.
3. Kery M, Schaub M (2012) Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press.
4. Toral GM, Stillman RA, Santoro S, Figuerola J (2012) The importance of rice fields for glossy ibis (Plegadis falcinellus): Management recommendations derived from an individual-based model. Biol Conserv 148: 19–27. Available: http://linkinghub.elsevier.com/retrieve/pii/S0006320712000936. Accessed 11 March 2012.
5. Donald PF (2007) Adult sex ratios in wild bird populations. Ibis (Lond 1859) 149: 671–692. Available: http://dx.doi.org/10.1111/j.1474-919X.2007.00724.x.
6. Charnov EL (1982) The Theory of Sex Allocation. Princeton University Press.
7. West SA (2009) Sex allocation. Princeton Univ Pr.
8. Caswell H (2001) Matrix population models. John Wiley & Sons, Ltd.
9. Stearns SC (1992) The evolution of life histories. Oxford University Press Oxford.
10. Lebreton J-DD, Burnham KP, Clobert J, Anderson DR (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol Monogr 62: 67–118.
11. Caswell H (2001) Matrix population models. John Wiley & Sons, Ltd.
12. Primack R (1995) A primer of conservation biology. Sunderland, MA: Sinauer Associates.
13. Lessells C (1991) The evolution of life histories. Behavioral ecology an evolutionary approach, 3rd edn. Oxford: Blackwell. pp. 32–68.
14. Nichols J, Ergon T (2009) Evolutionary Ecology. Modeling Demographic Processes In Marked Populations. Springer US. pp. 83–199.
15. Clobert J, Baguette M, Benton TG, Bullock JM (2012) Dispersal ecology and evolution. Clobert J, Baguette M, Benton TG, Bullock JM, editors Oxford University Press. Available: http://books.google.es/books?hl=es&lr=&id=wC9qnr4dH5AC&oi=fnd&pg=PP2&dq=dispersal+ecology+and+evolution&ots=o1vK8R4pFh&sig=_8o4y6mC1wpji-_Lsz4m5G_O1Lg. Accessed 9 December 2012.
16. Hanski I (1999) Metapopulation Ecology. Oxford University Press.
17. Newton I (2008) The migration ecology of birds. London: Academic Press, Elsevier. Available: http://scholar.google.es/scholar?q=ecology+of+migration+birds+newton&btnG=&hl=es&as_sdt=0,5#0#0. Accessed 25 August 2012.
18. Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, et al. (2012) Costs of dispersal. Biol Rev 87: 290–312. Available: http://www.ncbi.nlm.nih.gov/pubmed/21929715. Accessed 28 October 2012.
19. Matthysen E (2012) Multicausality of dispersal: a review. In: Clobert J, Baguette M, Benton TG, Bullock JM, editors. Dispersal Ecology and Evolution. Oxford University Press. pp. 3–18. Available: http://books.google.es/books?hl=es&lr=&id=wC9qnr4dH5AC&oi=fnd&pg=PA3&dq=dispersal+ecology+and+evolution+autor:matthysen&ots=o1vK8R4qFb&sig=cASjiEkoCWtoafZl6NOY50vKlY0. Accessed 9 December 2012.
20. Parmesan C (2006) Ecological and Evolutionary Responses to Recent Climate Change. Annu Rev Ecol Syst 37: 637–669. doi:10.2307/annurev.ecolsys.37.091305.30000024.

21. Le Galliard JF, Massot M, Clobert J (2012) Dispersal and range dynamics in changing climates: a review. In: Clobert J, Baguette M, Benton TG, Bullock JM, editors. Dispersal Ecology and Evolution. Oxford University Press. pp. 318–336. Available: http://books.google.es/books?hl=es&lr=&id=wC9qnr4dH5AC&oi=fnd&pg=PA317&dq=dispersal+and+range+dynamics+in+changing+climates:+a+review&ots=o1vKbP7qBk&sig=-ECj1erMn_-MCDEgAm-QjgZLnvs. Accessed 12 December 2012.
22. Pärn H, Saether B (2012) Influence of temperature on dispersal in two bird species. In: Clobert J, Baguette M, Benton TG, Bullock JM, editors. Dispersal Ecology and Evolution. Oxford University Press.
23. Baguette M, Legrand D, Fréville H, Van Dyck H, Ducatez S (2012) Evolutionary ecology of dispersal in fragmented landscape. In: Clobert J, Baguette M, Benton TG, Bullock JM, editors. Dispersal Ecology and Evolution. Oxford University Press. pp. 381–391.
24. Parmesan C, Ryrholm N, Stefanescu C, Hillk JK, Thomas CD, et al. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399: 579–583.
25. Jenouvrier S (2013) Impacts of climate change on avian populations. Glob Chang Biol: 1–22. Available: http://doi.wiley.com/10.1111/gcb.12195. Accessed 16 March 2013.
26. Foden W, Mace G, Vié J, Angulo A, Butchart S, et al. (2008) The 2008 Review of The IUCN Red List of Threatened Species. In: JC V, Hilton-Taylor C, Stuart S, editors. IUCN Gland. Switzerland.
27. Moreno J, Møller AP (2011) Extreme climatic events in relation to global change and their impact on life histories. Curr Zool 57: 375–389.
28. Hanski I, Gilpin ME (1997) Metapopulation biology: ecology, genetics and evolution. Available: http://www.lavoisier.fr/livre/notice.asp?ouvrage=1076225. Accessed 13 December 2012.
29. Pulliam H (1988) Sources, Sinks, and Population Regulation. Am Nat 5: 652–661.
30. Peery M, Becker B, Beissinger S (2006) Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird. Ecol Appl 16: 1516–1528. Available: http://www.ncbi.nlm.nih.gov/pubmed/16937815.
31. Lebreton J-D, Pradel R (2002) Multistate recapture models: modelling incomplete individual histories. J Appl Stat 29: 353–369.
32. Oro D, Ruxton GD (2001) The formation and growth of seabird colonies: Audouin's gull as a case study. J Anim Ecol 70: 527–535.
33. Doxa A, Besnard A, Bechet A, Pin C, Lebreton J-D, et al. (2013) Inferring dispersal dynamics from local population demographic modelling: the case of the slender-billed gull in France. Anim Conserv 16: 684–693. Available: http://doi.wiley.com/10.1111/acv.12048. Accessed 8 November 2013.
34. Balkiz Ö, Béchet A, Rouan L, Choquet R, Germain C, et al. (2010) Experience dependent natal philopatry of breeding greater flamingos. J Anim Ecol 79: 1045–1056.
35. Tims J, Nisbet I, Friar M, Mostello C, Hatch J (2004) Characteristics and Performance of Common Terns in Old and Newly-established Colonies. Waterbirds 27: 321–332.
36. Kildaw S, Irons D, Nysewander D, Buck C (2005) Formation and growth of new seabird colonies: the significance of habitat quality. Mar Ornithol 58: 49–58.
37. Coulson J, Coulson B (2008) Measuring immigration and philopatry in seabirds; recruitment to Black-legged Kittiwake colonies. Ibis (Lond 1859) 150: 288–299.

38. Martínez-Abraín A, Oro D, Jimenez J (2001) The dynamics of a colonization event in the european shag: the roled of immigration and demographic stochasticity. Waterbirds 24: 97–102.
39. Becker P, Bradley J (2007) The role of intrinsic factors for the recruitment process in long-lived birds. J Ornithol 148: 377–384. Available: http://link.springer.com/10.1007/s10336-007-0157-x. Accessed 11 September 2014.
40. Stamps J (1988) Conspecific Attraction and Aggregation in Territorial Species. Am Nat 131: 329–347.
41. Smith AT, Peacock MM (1990) Conspecific Attraction and the Determination of Metapopulation Colonization Rates. Conserv Biol 4: 320–323.
42. Oro D, Pradel R (2000) Determinants of local recruitment in a growing colony of Audouin's gull. J Anim Ecol 69: 119–132.
43. Danchin E, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79: 2415–2428.
44. Brown CR, Brown MB, Danchin E (2000) Breeding habitat selection in cliff swallows: the effect of conspecific reproductive success on colony choice. J Anim Ecol 69: 133–142.
45. Szostek K, Schaub M, Becker P (2014) Immigrants are attracted by local pre-breeders and recruits in a seabird colony. J Anim Ecol: 1–10. Available: http://www.ncbi.nlm.nih.gov/pubmed/24460741. Accessed 2 June 2014.
46. Brown CR, Brown MB (2001) Avian coloniality. Curr Ornithol Vol 16: 1.
47. Serrano D, Oro D, Ursúa E, Tella J (2005) Colony size selection determines adult survival and dispersal preferences: allee effects in a colonial bird. Am Nat 166: E22–31. Available: http://www.ncbi.nlm.nih.gov/pubmed/16032568.
48. Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the Allee effect. Trends Ecol Evol 14: 405–410. Available: http://www.ncbi.nlm.nih.gov/pubmed/10481205.
49. Stephens P, Sutherland W (1999) Consequences of the Allee effect for behaviour, ecology and conservation. Trends Ecol Evol 14: 401–405. Available: http://www.ncbi.nlm.nih.gov/pubmed/10481204.
50. Soutullo A, Limiñana R, Urios V, Surroca M, A Gill J (2006) Density-dependent regulation of population size in colonial breeders: Allee and buffer effects in the migratory Montagu's harrier. Oecologia 149: 543–552. Available: http://www.ncbi.nlm.nih.gov/pubmed/16794831. Accessed 22 September 2014.
51. Figuerola J, Mañez M, Ibáñez F, García L, Garrido H (2004) Morito común Plegadis falcinellus. Libro rojo de las Aves de España. Dirección general para la Biodiversidad. Madrid: SEO/BirdLife. pp. 74–76. Available: http://www.xoriguer.org/ftpdescarregues/libro_rojo_aves_espana.pdf#page=74. Accessed 22 August 2012.
52. Mañez M, Rendón-Martos M (2009) El morito común , la espátula común y el flamenco común en España . Población en 2007 y método de censo. Máñez M, Rendón-Martos M, editors Madrid: SEO/Birdlife.
53. Petersen CGI (1896) The yearly immigration of young plaice into the Limfjord from the German Sea. Rep Danish Biol Stn 6: 1–48.
54. Lincoln F (1930) Calculating waterfowl abundance on the basis of banding returns.
55. Thomson D, Cooch E, Conroy M (2009) Modeling demographic processes in marked populations. Vol. 3. New York: Springer.
56. Lebreton J, Nichols J, Barker R, Pradel R, Spendelow J (2009) Modeling Individual Animal Histories with Multistate Capture – Recapture Models. Adv Ecol Res 41: 87–173. Available: http://dx.doi.org/10.1016/S0065-2504(09)00403-6.

57. Lebreton J-D, Almeras T, Pradel R (1999) Competing events, mixtures of information and multistratum recapture models. Bird Study 46: 39–46. Available: http://www.tandfonline.com/doi/abs/10.1080/00063659909477230. Accessed 7 March 2012.
58. Pradel R (2005) Multievent: an extension of multistate capture-recapture models to uncertain states. Biometrics 61: 442–447. doi:10.1111/j.1541-0420.2005.00318.x.
59. Pradel R (2009) The stakes of Capture-Recapture Models with State Uncertainty. In: Thomson DL, Cooch EG, Conroy MJ, editors. Modeling Demographic Processes in Marked Populations. New York: Springer. pp. 781–795.
60. Leslie P (1945) On the Use of Matrices in Certain Population Mathematics. Biometrika 33: 183–212.
61. Fujiwara M, Caswell H (2002) Estimating population projection matrices from multi-stage mark–recapture data. Ecology 83: 3257–3265.
62. Sarrazin F, Legendre S (2000) Demographic Approach to Releasing Adults versus Young in Reintroductions. Conserv Biol 14: 488–500. Available: http://doi.wiley.com/10.1046/j.1523-1739.2000.97305.x.
63. Schaub M, Pradel R, Lebreton J (2004) Is the reintroduced white stork (Ciconia ciconia) population in Switzerland self-sustainable? Biol Conserv 119: 105–114. Available: http://linkinghub.elsevier.com/retrieve/pii/S0006320703004312. Accessed 19 September 2014.
64. Crouse D, Crowder L, Caswell H (1987) A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. Ecology 68: 1412–1423.
65. Besbeas P, Freeman S, Morgan B (2005) The potential of Integrated Population Modelling. Aust N Z J Stat 47: 35–48.

Capítulo I

Formation and growth of a heronry in a managed wetland in Doñana, southwest Spain

Simone Santoro[1], Manuel Mañez[2], Andy J. Green[1], and Jordi Figuerola[1]

1 Department of Wetland Ecology, Doñana Biological Station, C.S.I.C., Avda. Américo Vespucio s/n
41092 Seville, Spain.

2 Natural Processes Monitoring Team, Doñana Biological Station C.S.I.C., Avda. Américo Vespucio s/n 41092 Seville, Spain.

Short title: Creation and management of a heronry

Keywords: Ardea purpurea - Ardeola ralloides - Breeding colony - Bubulcus Ibis - Doñana - Egretta garzetta - Nycticorax nycticorax - Plegadis falcinellus - Population trends - Restoration - Wetlands

Santoro, S., Mañez, M., Green, A. J., & Figuerola, J. (2010). Formation and growth of a heronry in a managed wetland in Doñana, southwest Spain. Bird Study, 57(4), 515–524. doi:10.1080/00063657.2010.501371

Summary

We report the evolution of a new heron and ibis colony after the creation of three interconnected ponds ("Lucio de la FAO") in the early 1980's in Doñana Natural Space (DNS). Unlike the surrounding natural, temporary marsh, the FAO has extensive Typha beds used for nesting. After a drought, the Purple Heron, Squacco Heron and Glossy Ibis colonised the FAO in 1996. Night-Herons settled in 1998, while Cattle and Little Egrets were the last species to establish in the mixed colony in 2001.

The increase in the FAO has been particularly spectacular for Glossy Ibis (which had not bred in Doñana since 1958). Since the colony was established, the FAO has held a high proportion of all the pairs of these species in DNS, particularly of ibis and Squacco Herons. Since the first year of establishment in the FAO, numbers of ibis and Purple Herons have shown a significant growth trend in both the FAO and the rest of the DNS. However, on a longer time scale (since 1980), all species appear to have increased in the DNS. The FAO and its adjacent visitor centre have been a great success for conservation.

Introduction

Loss and degradation of wetlands are occurring worldwide and are particularly severe in the Mediterranean region, threatening many species of migratory birds (Moser et al. 1996; Gibbs 2000; Green et al. 2002; Cuttelod et al. 2008). To compensate for past and future wetland loss, it is important to investigate how management of remaining habitats and habitat restoration can enhance conservation of waterbirds.

In 1999, Doñana Natural Space (DNS, c. 108,087 ha), a protected area including the Doñana National Park and the Natural Park in southwest Spain (Fig. 1) was created. The area is also designated as a Biosphere Reserve (UNESCO), a Wetland of International Importance of the Ramsar Convention, an Important Bird Area (IBA), a World Heritage Site and a Natura 2000 site. The wetlands (c. 27.000 ha) of Doñana Natural Space, located in the Guadalquivir Marshes, have long been recognized as some of the most important for waterbirds in the Western Palaearctic (Chapman and Buck 1910). Doñana is particularly well known for its wintering waterbirds (Rendón et al. 2008), but it is also extremely important for breeding colonial waterbirds such as herons and ciconiformes (storks, ibises and spoonbills) (Máñez and Rendón-Martos 2009).

A steadily increasing proportion of remaining wetlands within the estuary of the river Guadalquivir have been protected since the 1960s, yet they are negatively affected by water extraction from the watershed, alien species, overgrazing, and other problems (García-Novo and Marín Cabrera 2005; Fernández-Delgado 2006). As a consequence, the extension of Bulrushes *Typha* spp. and Common Reeds *Phragmites australis* has undergone a major reduction in this area, limiting the area of suitable nest habitat for herons and ibises. This has been partially offset by the development of emergent vegetation in the FAO semi-artificial pond complex (Fig. 1), which

now holds a major mixed colony of Glossy Ibis *Plegadis falcinellus* and five heron species: the Squacco Heron *Ardeola ralloides*, Purple Heron *Ardea purpurea*, Little Egret *Egretta garzetta*, Cattle Egret *Bubulcus Ibis* and Night-Heron *Nycticorax nycticorax*. Glossy Ibis and Squacco Heron are found in the Spanish Red Data Book (Madroño et al. 2004) and other species are of conservation concern in Europe (BirdLife International 2004).

In this study, we analyzed a thirteen years dataset (1996-2008) of counts of colonial waterbirds in the FAO and the rest of the DNS. We aimed to: 1) describe the formation and build up of the FAO colony; 2) determine if this growth is related to increases in the overall number of breeding pairs in the DNS or alternatively to the redistribution of pairs already breeding in Doñana. Our working hypothesis was that there would be redistribution as indicated by negative correlations between numbers of pairs in the FAO and the rest of the DNS; 3) establish the influence of the flooded area of natural wetlands in the DNS (the major feeding habitat) on the number of breeding pairs ; 4) discuss the conservation implications of our findings.

Materials and methods

Study area

The "Lucio de la FAO" (37º04'N, 6º22'W) (Fig. 1) is a system of three interconnected ponds covering a total surface area of c. 50 ha and flooded by both direct precipitation and groundwater pumped from the underlying aquifer. Groundwater is pumped into the pond adjacent to "José Antonio Valverde Visitor Centre" (inaugurated in 1994) known as the "Lucio de las Casas" and then subsequently flows into the other two ponds via sluice gates. This artificial system was set up in 1981. The heronry is located in the "Lucio de las Casas" which provides dense vegetation cover suitable for nesting, especially *Typha* that is only present in this pond and is very scarce in the rest of Doñana. This pond also contains areas of *Tamarix* spp., which are the second most used nesting substrate. The other two ponds are almost free of emergent vegetation, probably due to the shallower depth, and higher variability in hydroperiod and salinity.

The visitor centre provides excellent views of the heronry and is one of the most interesting tourist attractions in Doñana (Fig. 2, the area can be observed from a webcam in the roof of the Centre: http://icts.ebd.csic.es/irListaCamarasAction.do). It is situated on the northern boundary of the park, with natural, temporary marshes to the south and mainly agricultural areas (including ricefields) to the north. The area of natural marshes varies greatly between years in response to rainfall fluctuations (Fig. 3), and in particularly dry years the FAO is one of the few areas holding water in the spring and summer. The herons and ibis in the colony feed mainly in the natural marshes lying to the south of the colony and in the nearby ricefields (see Macias et al. 2004; Montesinos et al. 2008 for details). The climate is Mediterranean sub-humid with rainy winters and dry summers (for more details of the study area see Serrano et al. 2006; Rendón et al. 2008; Kloskowski et al. 2009).

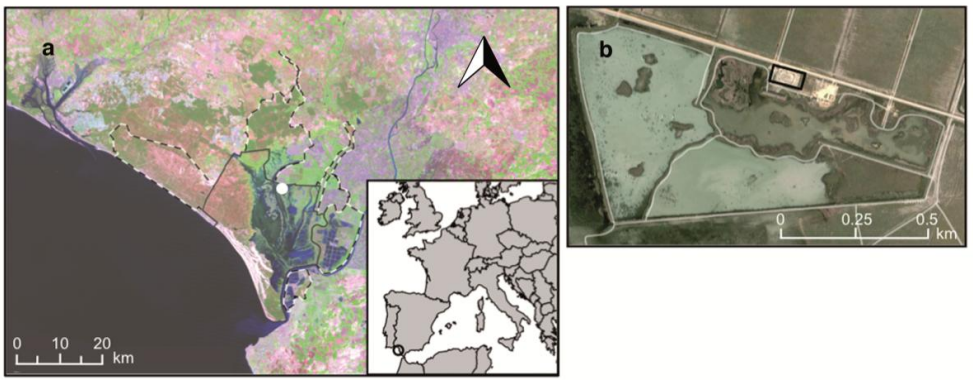

Fig. 1 Geographical location of the study area and satellite image of: a the Doñana Natural Space that includes the Natural Park (dashed lines) and the Doñana National Park (solid line). The white dot corresponds to the Lucio de la FAO; b the Lucio de la FAO showing the three ponds. The whole breeding colony nests in the pond closer to the José Antonio Valverde Visitor Centre (highlighted as a rectangle).

Survey methods

Since 1996, ornithologists from the Natural Processes Monitoring Team of Doñana Biological Station have annually estimated the number of pairs of the different species breeding in the FAO and other sites inside the DNS. This well-trained team checks systematically and exhaustively all the DNS from the ground and also uses light aircraft to improve estimates of population abundance and to search for new breeding colonies.

In the FAO, estimates were made by both counting nests during ringing operations and estimating visually the number of breeding pairs of each species from the visitor centre roof (about 100 m from the edge of the colony) and other vantage points. The proximity to the visitor centre permitted us to count the individuals on a very regular basis without disturbing the colony. We compared counts from ringing operations and vantage points to make the best estimates of the number of breeding pairs in the colonies. We used repeated counts performed throughout the breeding season to establish the minimum number of pairs of each species. Pairs that established later in the season tended to colonize new areas of

vegetation, facilitating estimation of the total number of nests and pairs in the colony.

Little bittern (*Ixobrychus minutus*) is abundant in the FAO (estimates range from a few pairs to a maximum of about 100 pairs in 2002) but data are not presented here owing to the greater methodological difficulties in counting of this species.

Fig. 2 a View of the breeding colony in the Lucio de la FAO from the **b** adjacent José Antonio Valverde Visitor Centre.

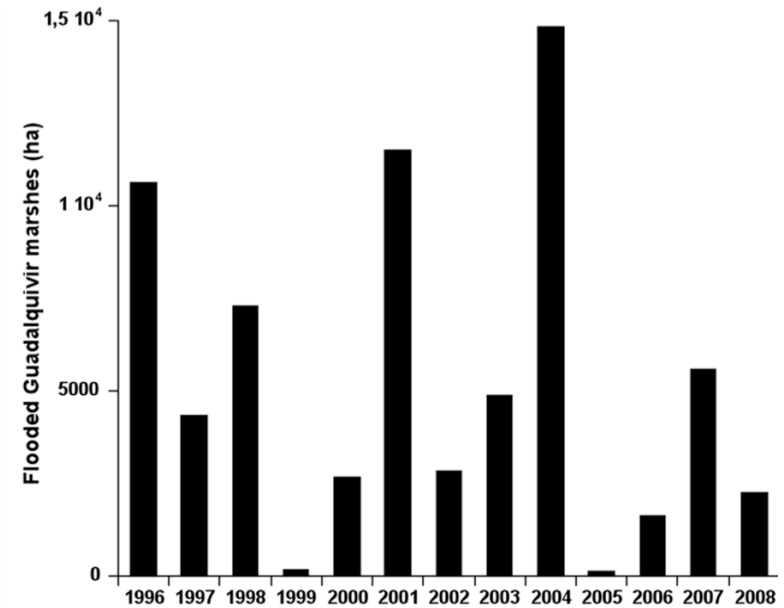

Fig. 3 Mean flooded area (ha) in June of marshes in Doñana National Park from 1996 to 2007.

Statistical analysis

In the 1980s some sporadic breeding by Purple Heron was recorded in the FAO, but it was not until 1996 that a reproductive colony of Glossy Ibis, Purple Heron and Squacco Heron became established. More recently, other species began to breed in the FAO: Night-Heron from 1998 and both Little and Cattle Egret from 2001. In the early 1990s, there were some failed breeding attempts by Glossy Ibis in the DNS (Mañez et al. 2009) but an extreme drought between 1991 and 1995 had a strong negative impact on all colonial waterbirds.

For each bird species, we tested for increasing or decreasing trends in the abundance of breeding pairs at FAO and in the rest of the DNS as well as in the whole DNS over the 13-year study period (1996-2008) with the non-parametric Mann-Kendall test (*MannKendall* function from *Kendall* package in R, McLeod 2005; R Development Core Team 2009).

There was a clear effect of drought years (1999 and 2005) on the breeding of waterbirds in Doñana when natural wetlands were almost dry and almost no pairs bred in the area (see Fig. 3 and Fig. 4). However, since our main interest was in detecting short-term linear trends for years when breeding was possible, we excluded these years from our analyses since they can be expected to reduce the chances of detecting population trends. Nevertheless, we report below those cases in which trends resulted qualitatively different when these drought years were also included in the analyses.

Temporal autocorrelation may potentially produce a spurious correlation between population size and time. Thus, for positively autocorrelated data, Hatfield et al. (1996) recommend to reject the null hypothesis unless the test is significant at $\alpha < 0.01$. Hence, we tested for autocorrelation in numbers of breeding pairs of each species in the Lucio de la FAO and in Doñana (*acf* function from *stats* package in R). Given that we investigated trends by excluding data from 1999 and 2005, we did the same when testing for autocorrelation.

As a measure of the relative importance of the FAO colony within the DNS as a whole, we calculated the mean percentage of all breeding pairs in the DNS that were present in the FAO, for each species and each year throughout the study period. Finally, to test how the population trend in the FAO was related to that in the rest of the DNS, we tested the correlation in population size between both areas for each species since the year of first breeding in the FAO (two-tailed Spearman rank correlation, *cor.test* function from *stats* package in R).

We tested for correlations between breeding populations in the whole DNS and the flooded area of temporary natural marshes during the breeding season (two-tailed Spearman rank correlation, *cor.test* function from *stats* package in R), using the mean flooded area for June (data from Remote Sensing and Geographic Information

Systems Lab, Doñana Biological Station - http://last-ebd.blogspot.com/). We performed these correlation analyses by including drought years, nevertheless we did not find any qualitatively different results when excluding those years.

Data were collected over 13 years, representing a limited sample size that may restrict our capacity to detect biologically relevant correlations. We thus calculated how large the correlation coefficient had to be for a two tailed correlation in order to be detectable with a power of 0.8 (i.e. so as to detect an existing correlation as significant in 80% of the analyses), using a significance threshold of 0.05 ("five-eighty convention", see Cohen 1988) and the sample sizes used in our analyses. Calculations were made in GPower 3.0.10 (Faul et al. 1996).

Results

Population dynamics

Apart from the near cessation of all breeding activity in the drought years 1999 and 2005, there was considerable variation in population dynamics between species and area (FAO versus the rest of the DNS, Fig. 4). A positive autocorrelation (lag = 1, r = 0.62, $p < 0.05$) was only recorded for Glossy Ibis in FAO. Even with a more restrictive value of α (0.01 instead of 0.05) we found a positive trend in size of the Glossy Ibis breeding population both in the FAO and the rest of the DNS, as well as in the whole of Doñana (Table 1). The breeding population of Purple Heron increased significantly in the Lucio de la FAO and in the whole DNS, but in the rest of the DNS its increase was marginally significant (Table 1). No other species showed significant trends over the period of study (Table 1).

When including drought years, trends were still significant for the Glossy Ibis in the FAO, the rest of the DNS, and in the whole DNS (respectively, $r_s = 0.66$, n = 13, p = 0.002, $r_s = 0.53$, n = 13, p = 0.02 and $r_s = 0.61$, n = 13, p = 0.004). Trends for Purple Heron were no longer significant although the trend in the FAO approached significance ($r_s = 0.42$, n = 13, p = 0.058).

Glossy Ibis was the species with the highest proportion of breeding pairs in the FAO, which held an overall mean of 86% of the DNS population. The Squacco Heron was also highly concentrated in the FAO (mean = 81.4%) while the Cattle Egret and Purple Heron were more variable in the extent of concentration at the FAO with high values in some years (e.g. 84.0% of Cattle Egret at FAO in 2008 and mean = 40.8%, 97.1% of Purple Heron in 2006 and mean = 35.6%). The FAO was less important for Little Egret and Night-Heron (means = 24.5% and 7.3%, of DNS pairs, respectively).

Contrary to our predictions, no negative correlations were found between the number of breeding pairs in the FAO and the rest of

Doñana, and positive correlations were recorded for two species: Glossy Ibis (r_s = 0.74, n = 13, p = 0.003) and Purple Heron (r_s = 0.74, n = 13, p = 0.003). Night-Heron and Squacco Heron breeding pairs in the FAO showed a marginally significant relationship to those outside (in that order, r_s = 0.56, n = 11, p = 0.07, r_s = 0.5, n = 13, p = 0.08). Numbers of Cattle and Little Egret in the FAO and rest of the DNS showed no relationship (respectively, r_s = 0.26, n = 8, p = 0.54, r_s = 0.17, n = 8, p = 0.70).

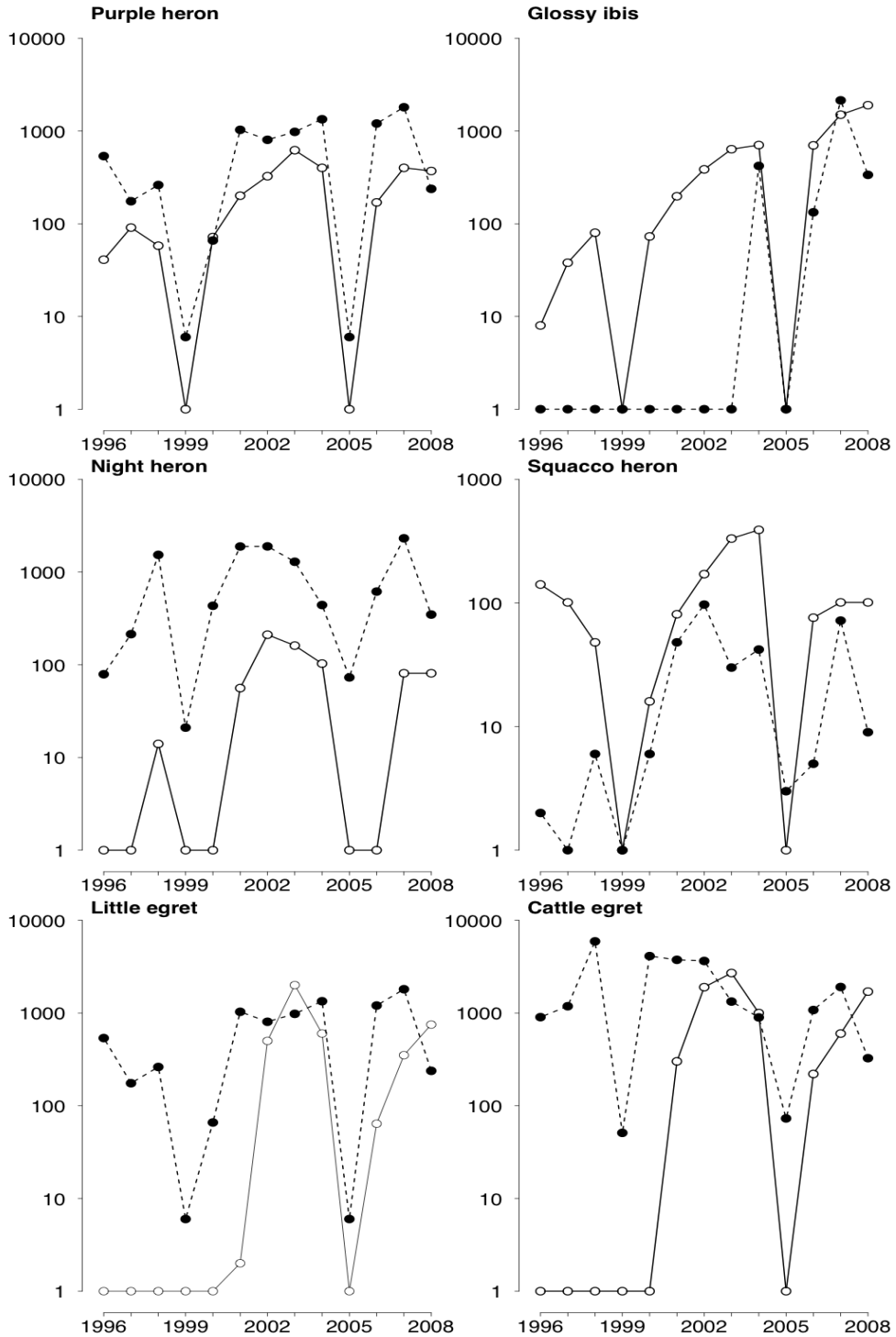

Fig. 4 Breeding population dynamics (log scale) in the Lucio de la FAO (open circles) and other colonies in the Doñana Natural Space (full circles). Note the change in scale on the y-axis.

Relationship with the flooded area

Contrary to our expectations, only three species showed a relationship between breeding numbers and the flooded area of natural marshes: Night-Heron (r_s = 0.74, n = 13, p = 0.005), Cattle Egret (r_s = 0.74, n = 13, p = 0.005) and Little Egret (r_s = 0.80, n = 13, p = 0.002). The other species showed positive but non-significant correlations with flooded area (Glossy Ibis: r_s = 0.33, n = 13, p = 0.26, Squacco Heron: r_s = 0.15, n = 13, p = 0.63, Purple Heron: r_s = 0.29, n = 13, p = 0.33).

Power analysis

Sample sizes used in our analyses, depending on the species and area considered, were: n = 7, 8, 9, 11, 13. From the smallest sample size to the highest, the minimum correlation coefficient detectable as statistically significant with a power of 0.80 would have been, respectively: r = 0.80, 0.77, 0.74, 0.69, 0.65.

Discussion

The Glossy Ibis was breeding in Doñana at the end of XIX century in small numbers and its abundance reduced abruptly until extinction in 1909, although some breeding attempts were recorded through the XX century (Valverde 1960; Castroviejo 1993). The reasons for local extinction could include the loss of habitats due to overexploitation and diversion for irrigation of the streams feeding the marshes (Serrano et al. 2006), as well as hunting pressure and other forms of human disturbance prior to the declaration of protected areas. Glossy Ibis was the species that took the best advantage of the Lucio de la FAO restoration and the one to show the strongest increase across the whole DNP since 1996 (Table 1). However, the recent colonization by Glossy Ibis of Spain is not only related to the creation of the FAO. Successful reproduction was recorded in 1994 in Valencia and, in 1996, simultaneously with the recolonization of Doñana, a smaller colony became established in the Ebro Delta (Figuerola et al. 2003). Still, the high productivity of the species in Doñana (Mañez et al. 2009) has probably fuelled further expansion in France (Kayser et al. 2008), Portugal (Equipa Atlas 2008) and Algeria (Boucheker et al. 2009).

The Lucio de la FAO has existed since the early 1980s, and there are various reasons that may explain why the breeding colony did not settle before 1996. The *Typha* beds were not planted but established slowly on their own, and had perhaps not reached sufficient cover and density in previous years. A particularly severe drought in 1991-1995 led to a strong reduction in the size of all breeding waterbird populations in Doñana. Furthermore, unknown external factors may have impeded the earlier establishment of glossy ibis or other species in the FAO (e.g. the status of breeding sites or low reproductive success elsewhere in the range of the

biogeographical population). Glossy Ibis tend to associate with other waterbirds, particularly herons, to breed (Davis and Kricher 2000). The presence of a growing population of Glossy Ibis may have drawn individuals of this and other species towards the FAO leading to the formation of a large, mixed colony (see review in Brown and Brown 2001).

The available evidence suggests that the creation of the FAO ponds and the suitable breeding habitat within has had a positive influence on the size of the bird populations in the whole of Doñana. This is supported by the strong positive trends in numbers of ibis and Purple Herons, and the lack of evidence for redistribution of breeding pairs to the FAO from elsewhere in the DNS. Furthermore, there has been a general increase in the numbers of all these species in Doñana since the late 1970s (Aguilera and Sañudo 1986; García et al. 1989; Mañez 1991) . The number of breeding pairs of some of these species in the FAO itself during our study period has been greater than the numbers found in the whole Doñana area in the 1980s. As indicated from our power analysis, the short period considered in the present study makes it hard to detect statistically significant population trends. Nevertheless, Glossy Ibis and Purple Heron showed significant increase during the study period.

The FAO has represented a new and important habitat suitable for herons and ibis, but aerial counts indicate long-term increases in wintering numbers of other wading birds (Grey Herons *Ardea cinerea*, White Storks *Ciconia ciconia*, Greater Flamingos *Phoenicopterus roseus* and spoonbills) in Doñana since 1978 (Rendón et al. 2008). None of these other species breed in the FAO, suggesting that there are also other causes to the long-term increases recorded for the species studied in this paper, such as increases in the surface area of artificial wetlands such as ricefields and fish ponds (see Rendón et al. 2008 for more discussion).

The positive correlation for Glossy Ibis between trends in the Lucio de la FAO and elsewhere in the Doñana Natural Space reflects the increase itself of the breeding population that affected simultaneously the number of pairs in the FAO and their redistribution in other sites inside Doñana. For the Purple Heron, some local population limitation due to scarcity of breeding sites may have been occurring prior to the creation of the FAO. Such a shortage could have been due to the lack of emergent vegetation in the rest of the DNS due to drought, water extraction and/or overgrazing (Soriguer et al. 2001; Manzano et al. 2005). Another factor promoting recent population increases is likely to be the fencing off of an area within the natural marshes in the DNS. In 1995 Juncabalejo, a *Phragmites* bed, was fenced off to provide protection against overgrazing and terrestrial predation (particularly wild boar *Sus scrofa*). Since then it has become an important breeding site for Purple Heron, ibis and other waterbirds, and this has probably contributed to the positive trends for these species outside the FAO.

Ideally, we should have studied the possible redistribution of birds between different colony sites using mark-recapture techniques. However, good mark-recapture data only exist for Glossy Ibis, and are strongly biased towards the FAO colony, given the practical advantages of ringing and observing there. These data confirm that ibis born in the FAO sometimes nest elsewhere in the DNS and vice versa. Nevertheless, the population increase recorded for this species in the FAO can not be explained by redistribution within DNS, since the Glossy Ibis started breeding in the FAO before beginning a later expansion to other parts of the DNS (Fig. 4).

The flooded area of natural marshes available as feeding habitat has a strong influence on all the species studied by preventing breeding during extreme drought conditions. Furthermore, there was a general positive relationship between the area of feeding habitat and the number of breeding pairs of Cattle Egret, Little Egret and

Night-Heron, suggesting strong local control of their population size. The Squacco Heron and Purple Heron did not show such a relationship, possibly because these are the species that chiefly winter away from Doñana (Registro ornitológico in: "Monitoring Group of Natural Processes of the Doñana Biological Station databases", http://www-rbd.ebd.csic.es/Seguimiento/mediobiologico.htm) and hence are more affected by conditions on their wintering grounds or migration routes. In Western Europe, the Purple Heron breeding population can be affected by drought conditions on the wintering grounds in tropical West Africa (Cavé 1983; den Held 1981). Similarly, the breeding population of Squacco Heron in Western Europe has been related to drought in the Sahel (den Held 1981; Hafner and Wallace 1988). Many Glossy Ibis winter locally in Doñana, and a relationship between breeding population and flooded marsh area will perhaps become apparent in the future when the general population growth phase is completed.

Overall, the management of the FAO wetlands has been very beneficial given the size of the breeding populations there and the conservation status of the species present (Table 2). The importance of the FAO is underlined by the high proportions of the entire Doñana populations that are breeding there. Additionally, the creation of the FAO has probably promoted the expansion of the Glossy Ibis across the Western Mediterranean and contributed to longer term increases in the breeding populations of other species.

Conservation and Management implications

Doñana is extremely important for the six bird species studied, with peak breeding populations greatly exceeding the 1% criteria used to identify wetlands of international importance (Table 2). Numbers of those species considered to be declining in Europe are particularly high in the DNS (Table 2). In terms of maximum counts during the period of study, the DNS holds more than 50% of the

Spanish breeding population of all species except the Cattle Egret and Squacco Heron (Table 2) which also have important breeding populations in the middle Tajo basin (see Garrido 2003).

The Jose Antonio Valverde visitor centre represents a successful example of wetland management with both ecological and educational (Fig. 2) functions. The creation of the FAO is particularly noteworthy for the reestablishment of the Glossy Ibis in the area, although it was not a specific initial management aim. This species is of conservation concern and in decline in Europe (Birdlife International 2004) and is considered IUCN Vulnerable in Spain (Figuerola et al. 2003) largely due to its concentration in a uniquely important colony at the FAO. The risk of epidemiological or catastrophic events makes the concentration of one species in a single locality a potential and serious threat for its conservation (IUCN, 2001). For example, toxic algae outbreaks occur in some years in the FAO and other parts of Doñana, resulting in catastrophic mortality to waterbirds (Alonso-Andicoberry et al. 2002; Lopez-Rodas et al. 2008).

Glossy Ibis and Squacco Heron are at risk by focusing their reproductive effort on one breeding site and thus it would be advisable to diversify the breeding habitat available for these species in Doñana. Although it is difficult to attract individuals from a good breeding site to another new one (Perennou 1996), the ongoing protection of additional areas in the DNS (e.g. Juncabalejo) from overgrazing by cows so as to permit the recovery of emergent vegetation is certain to benefit herons and ibis. The Glossy Ibis is already showing a tendency to reduce the proportion of breeding pairs in the FAO with respect to the rest of Doñana (Fig. 4), and Juncabalejo is increasing its importance for this and other species.

Acknowledgements

This study was possible thanks to the Doñana Biological Station Monitoring Team. In particular, we thank Luis García, Rubén Rodriguez, Fernando Ibañez, José Luis Arroyo, José Luis del Valle, Alfredo Chico and Hector Garrido. Thanks also to Carlos Urdiales, María Dolores Cobo and Juan Manuel Espinar for valuable information. We are especially grateful to the Laboratory of GIS and Teledetection (LAST-EBD) for providing data on marshes flooded area and other information. SS is supported by a JAE predoctoral grant from CSIC (co-funded by FEDER Program). Our research has been funded by the Regional Government of Andalusia (Junta de Andalucía) via the project *Las aves acuáticas de Doñana y el cultivo del arroz: la interacción entre la agricultura y la conservación de las zonas húmedas*.

References

Aguilera, E. & Sañudo, J. 1986. [Pasado y presente de las colonias de Ciconiformes en Doñana y Odiel.] *Bios* **2**:11-13 (in Spanish).

Alonso-Anisomery, C., García-Villada, L., Lopez-Rodas V. & Costas, E. 2002. Catastrophic mortality of flamingos in a Spanish national park caused by cyanobacteria. *Veterinary record* **151**:706-707.

BirdLife International (eds) 2004. *Birds in Europe: population estimates, trends and conservation status*. BirdLife International, Wageningen, The Netherlands.

Boucheker, A., Nedjah, R., Samraoui, Menaô, R. & Samraoui, B. 2009. Aspects of the Breeding Ecology and Conservation of the Glossy Ibis in Algeria. *Waterbirds* **32**:345-351.

Brown, C.R. & Brown, M.B. 2001. Avian coloniality: progress and problems. *Current Ornithology* **16**:1-82.

Castroviejo, J. 1993. [Mapa del parque nacional de Donana.] Consejo Superior de Investigaciones Cientificas (in Spanish).

Cavé, A.J. 1983. Purple Heron survival and drought in tropical West Africa. *Ardea* **71**: 217-224.

Chapman, A. & Buck, W.J. 1910. *Unexplored Spain*. E. Arnold, London.

Cohen, J. 1988. *Statistical Power Analysis for Behavioural Sciences*. Academic Press New York, New Jersey.

Cuttelod, A., García, N., Abdul Malak, D., Temple, H. & Katariya, V. 2008. The Mediterranean: a biodiversity hotspot under threat. In Vié, J.C., Hilton-Taylor, C. & Stuart, S.N. (ed.) *The 2008 review of the IUCN red list of threatened species*. IUCN Gland, Switzerland.

Davis, W.E. & Kricher, J. 2000. Glossy Ibis (*Plegadis falcinellus*). In Poole, A. & Gill, F. (ed.) *The Birds of North America*, Vol. 545. The birds of North America, Inc., Philadelfia.

Den Held, J.J. 1981. Population changes in the Purple Heron in relation to drought in wintering area. *Ardea* **69**:185–191

Equipa Atlas 2008. [Atlas das Aves Nidificantes em Portugal (1999–2005)] Instituto da Conservação da Natureza e da Biodiversidade, Sociedade Portuguesa para o Estudo das Aves, Parque Natural da Madeira e Secretaria Regional do Ambiente. Assírio & Alvim, Lisboa (in Portuguese).

Faul, F., Erdfelder, E., Lang, A. & Buchner, A. 1996. G*Power3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behav Res Methods* **39**:175–191.

Fernández-Delgado, C. 2006. Conservation management of a European natural area: Doñana National Park, Spain. In: Groom, M.J., Meffe, G.K. & Carroll C.R. (Third ed.) *Principles of conservation biology*, 536-543. Sinauer Associates Sunderland, Massachusetts.

Figuerola, J., Máñez, M., Ibáñez, F., García, L. & Garrido, H. 2003. [Morito Plegadis falcinellus.] In Martí, R. & del Moral J.C. (ed.) *Atlas de las Aves Reproductoras de España*. Dirección General de Conservación de la Naturaleza-SEO/BirdLife, Madrid (in Spanish).

Garrido, J.R. 2003. [Garcilla bueyera, *Bubulcus Ibis*.] In Martí, R. & del Moral J.C. (ed.) *Atlas de las Aves Reproductoras de España*. Dirección General de Conservación de la Naturaleza-SEO/BirdLife, Madrid (in Spanish).

García, L., Calderón, J. & Castroviejo, J. 1989. [Las aves de Doñana y su entorno.] EBD. CSIC. Cooperativa Marismas del Rocío (in Spanish).

García Novo, F. & Marín Cabrera, C. 2005. *Doñana, Water and Biosphere*. España: Confederación Hidrográfica del Guadalquivir, Ministerio de Medio Ambiente, Madrid.

Gibbs, J.P. 2000. Wetland loss and biodiversity conservation. *Conservation Biology* **14**:314-317.

Green, A. J., Hamzaoui, M. E., El Agbani, M. A. & Franchimont, J. 2002.The conservation status of Moroccan wetlands with particular

reference to waterbirds and to changes since 1978. *Biological Conservation* **104**:71-82.

Hafner, H. & Wallace, J.P. 1988. Population changes in Camargue Ardeids. The effect of climatic conditions in the wintering areas. *Bull. Col. Waterbirds Soc* 12-29.

Hatfield, J. S., Gould, W. R., Hoover, B. A., Fuller, M. R. & Lindquist, E. L. 1996. Detecting trends in raptor counts: power and type I error rates of various statistical tests. *Wildlife Society Bulletin* 505-515.

IUCN *Red List Categories and Criteria Version 3.1* 2001. IUCN Species Survival Commission. IUCN, Gland and Cambridge.

Kayser, Y., Gauthier-Clerc, M., Bechet, A., Poulin B., Massez G., Cherain Y., Paoli J., Sadoul N., Vialet E., Paulus G., Vincent-Martin N., Pilard P. & Isenmann P. 2008. [Compte rendu ornithologique camarguais pour les années 2001-2006.] *Revue d'Écologie* **63**:299-349 (in French).

Kloskowski, J., Green, A. J., Polak, M., Bustamante, J. & Krogulec, J. 2009. Complementary use of natural and artificial wetlands by waterbirds wintering in Doñana, south-west Spain. *Aquatic Conservation: Marine and Freshwater Ecosystems* **19**:815-826.

Lopez-Rodas, V., Maneiro, E., Lanzarot, M. P., Perdigones, N. & Costas, E. 2008. Mass wildlife mortality due to cyanobacteria in the Donana National Park, Spain. *The Veterinary record* **162**:317-318.

Macías, M., Green, A.J. & Sánchez, M.I. 2004. The Diet of the Glossy Ibis During the Breeding Season in Doñana, Southwest Spain. *Waterbirds* **27**:234-239.

Madroño, A., González, C. & Atienza, J.C. 2004. [Libro Rojo de las Aves de España.] DGB (MIMAM) & SEO/BirdLife. Madrid (in Spanish).

Manzano, M., Custodio, E. & Mediavilla, C. 2005. Effects of localised intensive aquifer exploitation on the Doñana wetlands (SW

Spain). In Intern. Assoc. of Hydrogeologists, Selected Papers, Vol. 7. *Intensive Use of Groundwater*. Balkema.

Máñez, M. 1991. [Estado actual en el Parque Nacional de Doñana de las especies de aves incluidas en la Lista Roja de los Vertebrados de Españadentro de las categorías "En peligro" y "Vulnerable".] In Andalus, Fundación Bios y Finca el Retiro. *Actas de las I Jornadas sobre Zonas Húmedas Andaluzas. Fuente de Piedra, abril 1990*. 41-49. Málaga, Spain (in Spanish).

Máñez, M. & Rendón-Martos, M. (eds) 2009. [*El morito, la espátula y el flamenco en España. Población en 2007 y método de censo.*] 12-32. SEO/BirdLife. Madrid, Spain (in Spanish).

McLeod, A.I. 2005. Kendall: Kendall rank correlation and Mann-Kendall trend test. R package version 2.0. http://www.stats.uwo.ca/faculty/aim

Montesinos, A., Santoul, F. & Green, A.J. 2008. The diet of the Night-Heron and Purple Heron in the Guadalquivir marshes. *Ardeola* **55**:161-167.

Moser, M., Prentice, C. & Frazier, S. 1996. A global overview of wetland loss and degradation. In UNFCCC (ed.) *Technical Session B of the Ramsar Conference of Parties (COP)*. 253–260, New York, NY, USA and Brisbane, Australia.

Perennou, C., Sadoul, N., Pineau, O., Johnson, A. & Hafner, H. 1996. Management of nest sites for colonial waterbirds. In Tour du Valat (ed.) *Conservation of Mediterranean Wetlands No.4*. Arles. France

R Development Core Team 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rendón, M. A., Green, A. J., Aguilera, E. & Almaraz, P. 2008. Status, distribution and long-term changes in the waterbird community wintering in Doñana, south–west Spain. *Biological Conservation* **141**:1371-1388.

Serrano, L., Reina, M. & Martín, G. 2006. The aquatic systems of Doñana (SW Spain): watersheds and frontiers. *Limnetica* **25**:11-32.

Soriguer, R.C., Rodríguez Sierra, A. & Domínguez, L. 2001. [*Análisis de la incidencia de los grandes herbívoros en la marisma y vera del Parque Nacional de Doñana*.] Organismo Autónomo de Parques Nacionales, Madrid, Spain (in Spanish).

Valverde, J.A. 1960. [Vertebrados de las marismas del Guadalquivir.] In CSIC (ed.) *Archivos del Instituto de Aclimatación*, Vol. 9:1-168. Almería, Spain (in Spanish).

Wetlands International 2006. *Waterbird Population Estimates* (fourth ed.)
Wetlands International, Wageningen, The Netherlands.

Tables

Population trends

Table 1

Species	Locality								
	Lucio de la FAO			Rest of DNS			DNS		
	tau	p	N	tau	p	n	tau	p	n
Glossy Ibis	+0.93	<0.0001	11	+0.67	0.009	11	+0.89	0.0002	11
Night-Heron	+0.11	0.75	9	+0.27	0.28	11	+0.27	0.28	11
Squacco Heron	+0.15	0.58	11	+0.37	0.14	11	+0.2	0.44	11
Cattle Egret	-0.05	1	7	-0.34	0.16	11	-0.09	0.76	11
Little Egret	+0.24	0.55	7	-0.27	0.28	11	-0.09	0.76	11
Purple Heron	+0.59	0.015	11	+0.42	0.087	11	+0.49	0.043	11

Trends of populations (nº of pairs) breeding in the Lucio de la FAO, in the rest of the Doñana Natural Space and in the whole Doñana Natural Space, based on breeding season counts from 1996 to 2008. Two drought years (1999 and 2005) when there were few or no breeding pairs in the area have been excluded from the analysis. The number of years considered varies for the FAO because some species did not begin breeding until 1998 or 2001.

4
5

Conservation importance

Table 2

Species	Locality				Status in Europe	1% Spain	1% Biog. population
	FAO		DNS				
	Min	Max	Min	Max			
Glossy Ibis	7	1900	7	3643	Declining	4	570
Night-Heron	13	210	78	2391	Depleted	33	790
Squacco	15	389	20	430	Declining	10	40
Cattle Egret	219	2700	902	5930	Secure	600	2800
Little Egret	1	2000	496	7816	Secure	150	1300
Purple	40	620	136	2206	Declining	20	120

Species abundance in Lucio de la FAO and the whole Doñana National Park and their conservation importance. Minimum and maximum number of breeding pairs in the FAO colony and in the whole DNP between 1996 and 2008 are reported. For each species the number of DNP breeding pairs is only reported for years when there were breeding pairs in the FAO colony. Values for dry years (1999 and 2005) are not considered. Conservational status in Europe is from BirdLife International (2004) where the overall trend in the entire European region is taken in account. The 1% thresholds are based on the estimated size of Spanish breeding (mean estimates of pairs between 1998 and 2002 - BirdLife International, 2004) and bio-geographical wintering populations (Wetlands International, 2006).

CAPÍTULO 2

Facultative and non-facultative sex ratio adjustments in a dimorphic bird species

Simone Santoro* [1], Andy J. Green[1], John R. Speakman[2,3] and Jordi Figuerola[1]

[1] Department of Wetland Ecology, Doñana Biological Station-CSIC, Américo Vespucio s/n, 41092, Seville, Spain

[2] Institute of Environmental and Biological Sciences, University of Aberdeen, Aberdeen, UK

[3] State Key Laboratory of Molecular Developmental Biology, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing, China

Keywords: sex allocation, energy expenditure, Doñana, equal allocation hypothesis, population dynamics

Santoro, S., Green, A. J., Speakman J. R. & Figuerola, J. (in press). Facultative and non-facultative sex ratio adjustments in a dimorphic bird species. OIKOS doi: 10.1111/oik.01889

Summary

If parental allocation to each offspring sex has the same cost/benefit ratio, Fisher's hypothesis predicts a sex ratio biased towards the cheaper sex. However, in dimorphic birds there is little evidence for this, especially at hatching.

We investigated the pre-fledgling (*i*) sex ratio, (*ii*) body condition and (*iii*) sex-differential mortality in a population of the glossy ibis (*Plegadis falcinellus*), in southern Spain between 2001 and 2011. We defined two age groups for the period between hatching and fledging. We also compared pre-fledgling with the autumn sex ratio. Metabolic rates were estimated by the Doubly Labeled Water (DLW) technique to establish that sons (the bigger sex) were 18% more energy demanding than daughters, and to compute the predicted Fisher's sex ratio (0.465). As population size increased between years, body condition decreased in both sexes, and mortality increased more for daughters than sons prior to fledging. At the same time, the proportion of males among chicks close to fledging increased (average sex ratio: 0.606) while the proportion close to hatching decreased (average sex ratio: 0.434, in line with Fisher's prediction). Furthermore, the proportions of males at fledging and the following autumn were negatively correlated across years.

We suggest that, as population density increased and conditions worsened the larger sex had relatively higher survival. These differences in survival produce a shift from a facultative female-biased sex ratio at hatching into a non-facultative male-biased sex ratio of fledglings. Additionally, the excess of males at fledging was counterbalanced by sex-related dispersal during the autumn. Overall, glossy ibis sex ratio is a product of a combination of facultative and non-facultative adjustments triggered by environmental conditions, driven by rapid population growth, and mediated by highly interrelated life-history traits such as body condition, mortality, and dispersal.

Introduction

Differential sex allocation occurs when different amounts of resources are devoted to sons and daughters, which can bias the sex ratio, an important life-history trait, at the individual and/or population level. Even though clear-cut boundaries are not well defined (West 2009), sex ratio is usually studied at three different stages: primary (at fertilization), secondary (at birth) and tertiary (at sexual maturity). However, differential mortality or dispersal of sons and daughters can also cause shifts in sex ratio in between these stages.

Since Darwin (Darwin 1871) addressed this topic, several evolutionary theories and empirical studies have been proposed (reviews in Hardy et al. 2002; West 2009). Fisher's landmark equal allocation theory (Fisher 1930) aimed to explain the common occurrence of balanced sex ratios in nature by postulating that, if fitness cost/benefit ratios are not sex dependent, parents should invest the same in daughters and sons. Thus, provided both daughters and sons have the same cost for parents, frequency-dependent selection would offset every deviation from parity and lead to a balanced, evolutionary stable sex ratio. On the other hand, when the sexes require different amounts of resources, selection would skew the sex ratio towards the cheaper sex, if identical parental allocation for each sex was maintained.

Other theories have been developed by considering situations where there are different costs and benefits of male and female offspring, when sex allocation should be adjusted to maximize fitness. There are two main theoretical frameworks: i) one postulating that parents should adjust offspring sex ratio depending on predictable sibling cooperation or competition (Local Mate Competition; Hamilton 1967, Local Resource Competition; Clark 1978, Taylor & Bulmer 1980, or Local Resource Enhancement; Emlen, Emlen & Levin 1986, Lessells & Avery 1987), and ii) one proposing that adaptive sex ratio

adjustments depend on the specific conditions of parents (Trivers and Willard 1973). In birds, although a number of alternative explanations coexist (reviewed in West 2009), linear (Wiebe and Bortolotti 1992, Appleby et al. 1997, Arroyo 2002) or non-linear (Millon and Bretagnolle 2005) relationships between environmental covariates and sex ratio have often been interpreted as supporting the Trivers & Willard hypothesis.

Given the central role offspring costs play in sex allocation theories, dimorphism has often been considered a proxy for different rearing costs (Trivers and Hare 1976, Clutton-Brock et al. 1985, Magrath et al. 2007), and sexually size dimorphic species have been used as models for testing sex allocation theories (e.g. Stamps 1990; Anderson et al. 1993; Torres & Drummond 1999). Nevertheless, the relationship between sexual size dimorphism and differential costs has rarely been demonstrated (but see Magrath et al. 2007). In species with parental care, sex allocation refers to the resources (time and energy) parents devote to their offspring (Komdeur 2012). As well as dimorphism, differential mortality during the parental care period can alter the costs of each offspring sex, provoking facultative modification in primary sex ratio but also facultative and non-facultative sex ratio variation at the time of fledging (Leigh 1970, West 2009). For instance, if offspring of the larger sex suffer higher mortality then the difference in raising costs between the larger and smaller sex would be reduced (because of shorter parental care time, Komdeur 2012). This might explain why, in dimorphic birds, there is more support for Fisher's prediction at fledging than at hatching (Pen et al. 2000, Benito and González-Solis 2007). Also, if differential mortality is determined by environmental factors and not by facultative manipulation, the sex ratio at fledging can be biased in the opposing manner to that predicted by theory (Dhondt and Hochachka 2001). In such a scenario, sex-related dispersal could provide a facultative mechanism to offset a maladaptive sex ratio.

The body condition of chicks can be related to food availability and/or quality, competition for resources, and parasite load. While a direct relationship with these factors can be difficult to be ascertain, these processes can be mediated by population density (reviewed in Brown & Brown 1996). Two opposing hypotheses have been postulated to explain how population density may affect access to resources (reviewed in Brown & Brown 2001): i) the enhanced foraging efficiency hypothesis, which predicts that at high density the access to resources is facilitated by some behavioral change (e.g. Ward & Zahavi 1973; Allainé 1990), and ii) the increased competition hypothesis which posits that, as population size increases, foraging efficiency declines (e.g. Tella et al. 2001; Dann & Norman 2006). Body condition of chicks can also depend on increasing parasite load (e.g. Merino & Potti 1995) which can increase along with colony size (Brown and Brown 1986, Rózsa et al. 1996). According to the 'Silver Spoon' hypothesis (Grafen 1988), conditions at an early life-stage affect the individual fitness, as confirmed by many empirical studies (e.g. Van de Pol et al. 2006; Stamps 2006). Thus, following the above rationale, the body condition of chicks might change the sex-related costs and benefits (Kruuk et al. 1999, Wilkin and Sheldon 2009), and therefore cause adaptive sex ratio adjustments.

The present study was centered on sex ratio variation and its underlying causal mechanisms in the Glossy Ibis (Plegadis falcinellus), a dimorphic species nesting in Doñana (SW Spain) (Santoro et al. 2010) where it has undergone an explosive population expansion from 7 pairs in 1996 to more than 7,000 pairs by 2011. Only population-level data on sex-ratios were available because the chicks, cared for by both parents, leave the nest and form creches when they are two weeks old (Cramp and Simmons 1977) and collection of brood-level data at an earlier stage was not feasible because of potential disturbance to the breeding colony (Götmark 1992).

We aimed to investigate: (i) if male chicks had greater energetic requirements than females, as expected from their larger size at fledging, (ii) if pre-fledgling sex ratio departed from that expected from simple chromosomal assortment (1:1) or from Fisher's equal allocation theory (according to the estimated energetic requirement of each sex), (iii) if pre-fledgling sex ratio, sex-specific body condition or sex-differential mortality depended on colony size or other proxies for the availability of resources, and (iv) if the pre-fledgling and autumn sex ratios were inversely related as expected if dispersal counterbalances the excess of one sex amongst offspring. Since time elapsed from hatching can affect the proportion of males by differential mortality, we tested the sex ratio hypotheses by considering pre-fledglings either as a whole or divided into two subgroups according to their age.

Methods

Study Area, Field Data

The "Lucio de la FAO" ("FAO" hereafter) hosts the main Glossy Ibis colony at Doñana, a protected area in SW Spain (Santoro et al. 2010, Ramo et al. 2013). Here, seven pairs settled in 1996 and since then this species has regularly nested in the area, except for three years (1999, 2005 and 2012) when drought events prevented them from breeding owing to an absence of foraging habitat. At the FAO colony, the number of breeding pairs has increased dramatically (more than 2,000 pairs in 2011) and since 2004, additional breeding sites were occupied by this species in Doñana, hosting about 4,000 pairs in 2011 (Ramo et al. 2013).

Chicks were molecularly sexed (Griffiths et al. 1998) from samples obtained during ringing operations at the main colony (Santoro et al. 2010). Samples were obtained by either 1) pulling of one outer rectrix or 2) taking a sample of blood from the medial metatarsal vein.

Statistical analyses

If sex-differential mortality occurred during the parental care period, then we would expect to find a different sex ratio at hatching and at fledging, and therefore observe differences in sex-ratio between younger and older pre-fledglings. For this reason, we defined two subgroups according to age. As a proxy for an individual's age regardless of sex, we used the wing length, a non dimorphic measure in this species (Figuerola et al. 2006). Wing length has been shown for other bird species to be relatively unaffected by nutritional status and a good proxy for age of chicks (Gaston 1985, Benowitz-fredericks and Kitaysky 2005). We considered the younger group to be those whose wing length was equal to or shorter than the overall median (sexes combined). Then,

ecological hypotheses on sex ratio variation were tested using pre-fledgling sex ratio for the two age groups separately as well as on the whole data set.

All statistical analyses in this study were implemented in R version 3.0.2 (R Development Core Team 2013). The sample size and the number of degrees of freedoms for each hypothesis tested differed according to the data available for the specific set of variables.

DNA-sampling procedure: effect on sex ratio and body condition

Whereas pulling a feather is a straightforward task and requires a short handling time, bleeding a chick is a more time demanding (Magrath et al. 2007) and specialized task providing a larger blood sample suitable for other studies. Thus, a systematic tendency to avoid bleeding smaller or less healthy-looking individuals may exist. To check if this was a source of bias for our study, we compared the sex ratio and body condition observed in chicks that were bled against those from which a feather was pulled. We assumed the latter to be completely random with respect to sex and body condition, because all chicks encountered outside nests were ringed, and feathers were taken from as many of these as time allowed.

As a body condition index, we used the Scaled Mass Index (SMI) which has several advantages over alternative methods (Peig and Green 2009, 2010), and which performs well in birds (Bókony et al. 2012, Guillemain et al. 2013). Given that Glossy Ibis chicks are sexually dimorphic (Figuerola et al. 2006), the SMI was calculated separately for each sex using measures of body mass and tarsus length (details in Appendix A1).

First, to test the hypothesis that sampling by bleeding biased the sex ratio estimates, we considered a subset of our data drawn from colony visits ("field-sessions" hereafter) in which both sampling

procedures were used (nfeather= 1080, nbleeding= 597, nsessions= 24, nyears= 7). We ran a binomial GLMM (glmer function from package lme4; Bates et al. 2012) considering the sex ratio (number of males out of total number of sampled chicks) as response variable (cbind function; Wilson & Hardy 2002), the year as a random factor and the sampling procedure as an explanatory variable. We also aimed to rule out the possibility that the effect of sampling procedure on sex ratio was due to a procedure-related propensity to select individuals of different ages, for which different sex ratios might exist. Thus, we ran a binomial GLMM considering the sex of an individual sex as response variable, field-sessions nested within year as random effects and the sampling procedure and wing length (a proxy for age) as predictors together with their interaction. We used a subset of data from years for which both sampling procedures had been used, and wing length was measured (nfeather= 637, nbleeding= 459, nsessions= 8, nyears= 5).

Secondly, to test the effect of sampling procedure on the body condition index we performed a gaussian LMM (lme function from package nlme ; Pinheiro et al. 2013) on a subset of data for which both bleeding and feather samples were available in each field-session (nfeather:females= 321, nfeather:males= 316, nbleeding:females= 174, nbleeding:males= 285, nsessions= 8, nyears= 5). We considered the average body condition of each sex for each field-session and sampling procedure as the response variable, year as a random factor, and sex, sampling procedure and their interaction as predictors. The LMM was weighted for the number of replicates from which average values of body condition were calculated for each field-session.

Energetic requirements of male and female chicks

Daily Energy Expenditure (DEE) was estimated using the DLW technique (Butler et al. 2004). We fenced a small section of the colony (50 x 50 meters) using a plastic wire mesh (1.5 m high) from May 20th to May 25th 2009. Forty-six chicks (20 females and 26 males) were injected intraperitoneally with 0.5 ml of 2H- and 18O-enriched water (Speakman 1997). All the dose syringes were weighed to four decimal places prior and post administration using an electronic precision balance. After being injected, chicks were retained in shaded and ventilated cardboard boxes during an hour, to allow isotopes to reach equilibrium (Król and Speakman 1999), then a first blood sample was taken and the chicks were released inside the fenced area. A second blood sample was taken after 48/72 hours (fieldwork sessions on 20th, 22nd and 25th May) to estimate the isotope elimination rate and minimize the influence of circadian deviation in DEE (Speakman and Racey 1988). Taking samples over multiple days minimizes the substantial day to day variance in DEE (Speakman et al. 1994, Berteaux et al. 1996). Four individuals were blood-sampled without prior injection to estimate background isotope enrichments of 2H and 18O (Speakman & Racey 1987: method D). Blood samples were immediately heat sealed into 2 x 100µL glass capillaries. Capillaries that contained the blood samples were then vacuum distilled (Nagy 1983), and water from the resulting distillate was used to produce CO2 and H2 (methods in Speakman et al. 1990 for CO2 and Speakman & Król 2005 for H2). The isotope ratios 18O: 16O and 2H: 1H were analyzed using gas source isotope ratio mass spectrometry (Optima, Micromass IRMS and Isochrom µG, Manchester, UK). Samples were run alongside three lab standards for each isotope (calibrated to International standards) to correct delta values to ppm. Isotope enrichments were converted to values of daily energy expenditure using a single pool model as recommended for this size of animal by Speakman (1993). There are several alternative

approaches for the treatment of evaporative water loss in the calculation (Visser and Schekkerman 1999). We chose the assumption of a fixed evaporation of 25% of the water flux (equation 7.17: Speakman 1997), which has been established to minimize error in a range of conditions (Visser and Schekkerman 1999, Van Trigt et al. 2002).

No knowledge about potential differences in fledging times between sexes exists in this species, and samples were collected from chicks of different ages. For these reasons, we assumed differences between sexes in estimated DEE reflected differences in total expenditure, and considered them as proxies of investment in sons and daughters (Magrath et al. 2007).

We tested for sexual differences in DEE using linear regression models with type III sum of squares (function lm from package car). We used DEE as response variable and sex and wing, or sex and body mass, as predictors. Unlike wing length, body mass is highly dimorphic among Glossy Ibis chicks (Figuerola et al. 2006).

Pre-Fledgling sex ratio: departure from parity and Fisher's hypothesis

According to Fisher's argument, natural selection favors equal allocation in both sexes, hence, it is expected that:

$$nF \times c\overline{F} = nM \times c\overline{M} \quad (eq.\ 1)$$

Where $c\overline{F}$ and $c\overline{M}$ represent the average costs of raising one female and one male respectively, and nF and nM the number of males and females (adapted from Charnov 1982). By simple algebra, it can be shown that predicted sex ratio according to *eq. 1* is:

$$\frac{nM}{nM + nF} = \frac{c\overline{F}}{c\overline{F} + c\overline{M}} \quad (eq.\ 2)$$

Thus, in the case where the average costs of rearing a female and a male are identical ($c\overline{F} = c\overline{M}$), the expected sex ratio equals 0.5 and Fisher's argument cannot be distinguished from simple meiotic

sex determination (Griffiths et al. 1998, Harvey et al. 2006). On the contrary, if $\bar{c}_F \neq \bar{c}_M$, then the predicted sex ratio is not balanced and its value can be estimated by *eq. 2*.

We used the average DEE value of females and males as proxies for the average costs of raising daughters and sons respectively, to calculate the predicted sex ratio according to Fisher's equal allocation theory (eq. 2). Then, we computed yearly sex ratio values as the proportion of male fledglings within the total sample of sexed chicks.

We tested if the sex ratios observed in different years deviated from those predicted according to the Fisher' and Random Assortment hypotheses by using a one-sample t-test on the yearly differences between observed and predicted sex ratios.

Environmental covariates and relationship with pre-fledgling sex ratio, body condition and sex-differential mortality

We examined the correlations between breeding population size or the surface area of flooded marshes on the one hand, and the pre-fledgling sex ratio, body condition of each sex, and sex-differential mortality on the other. Marsh area is a measure of the amount of feeding habitat available (see Santoro et al. 2010 for details), and is dependent on winter rainfall which itself has a positive effect on population growth (Ramo et al. 2013). A preliminary analysis showed that, whereas the yearly average wing length of male chicks increased linearly from 2002 to 2011 ($t = 4.2$, d.f. = 5, $r = 0.88$, $p < 0.05$), that of females did not ($t = 0.98$, d.f. = 5, $r = 0.40$, $p = 0.38$). Thus, assuming that there was no bias from the research staff towards collecting data from older individuals as time progressed, we used the yearly average difference between wing lengths of male and of female chicks as a proxy of sex-differential mortality ("sex-biased mortality" hereafter). Additionally, in cases where we found a significant correlation between body condition and other variables, we

tested for a difference between sexes by comparing the two slope coefficients with the Z test (Cohen et al. 2003). We did the same to compare slopes between age groups when there was a significant correlation between sex ratio and colony size.

Pre- and post-fledgling sex ratios

We tested the correlation between pre- and post-fledgling sex ratios. Since we aimed to test if the sex ratio close to the fledging time was inversely related to the autumn sex ratio, we tested this relationship on all the pre-fledglings (regardless of age) and those closer to fledging. As estimates of post-fledgling sex ratio, we used estimates from capture-recapture analyses performed in Santoro, Green & Figuerola (2013) on individuals first resighted between October and December of each year.

Results

Effect of DNA sampling procedure on sex ratio and body condition

The probability that an individual was a male was higher among those whose DNA was obtained by bleeding than those which were feather-sampled (slope ± S.E. = 0.5±0.1, z = 4.78, $P < 0.001$). After controlling for the age effect proxied by wing length, the sampling procedure still had an effect on sex of individuals sampled (*wing*, slope ± S.E. = 0.40±0.065, z = 6.23, $P < 0.001$; *sampling procedure*, slope ± S.E. = 0.34±0.12, z = 2.91, $P < 0.01$; *sampling procedure:wing*, slope ± S.E. = 0.19±0.13, z = 1.44, $P = 0.15$). However, we did not find any effect of sampling procedure on body condition estimates after controlling for the effect of sex (*sampling procedure*, slope ± S.E. = 0.02±0.03, t = 0.64, $P = 0.56$; *sex*, slope ± S.E. = -0.06±0.03, t = -1.94, $P < 0.05$; *sampling procedure:sex*, slope ± S.E. = -0.003±0.05, t = -0.07, $P = 0.94$). To avoid any bias due to sampling procedure, further analyses on sex ratio and on sex-differential mortality were performed using only individuals sexed from feather samples.

Daily Energy Expenditure of female and male chicks

Estimated DEE was higher in males than in females (mean ± S.D.: 510.36±15.2 kJ day^{-1} vs. 442.96±13.3 kj day^{-1}) after controlling for wing size (*sex*, estimate ± S.E. = 67.40±20.52, $F_{1,43} = 10.78$, $P < 0.01$; *wing*, slope ± S.E. = 1.39±0.64, $F_{1,43} = 4.7$, $P < 0.05$; Fig. 1). However, such differences disappeared when controlling for body mass (*sex*, slope ± S.E. = 21.64±20.95, $F_{1,43} = 1.07$, $P = 0.31$; *body mass*, slope ± S.E. = 0.74±0.16, $F_{1,43} = 21.8$, $P < 0.001$), which was the best predictor of DEE regardless of individual sex.

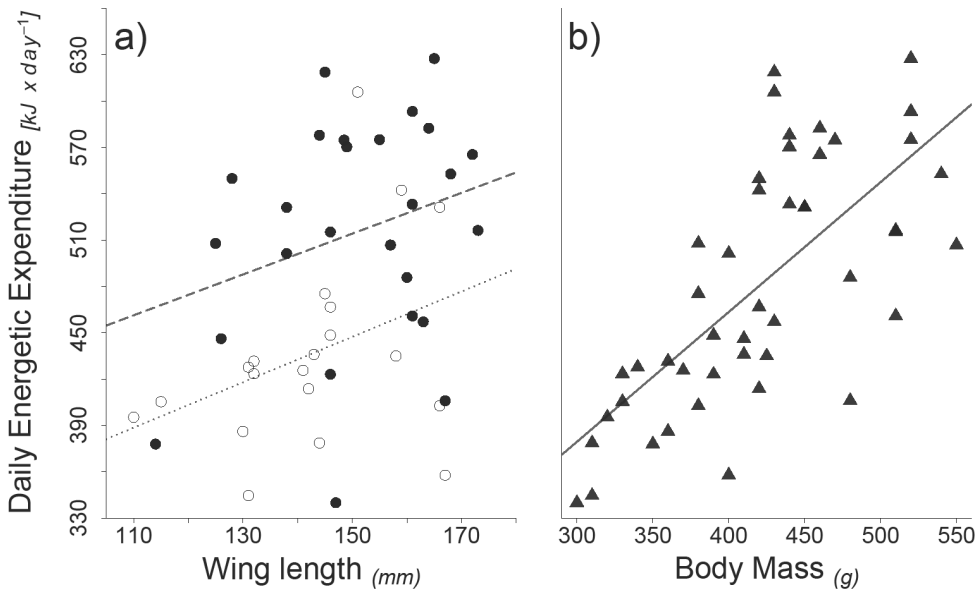

Figure 1. Metabolic costs of female and male chicks. a) Linear relationship of female (empty circles - dotted line) and male (full circles - dashed line) chick wing length with Daily Energy Expenditure (DEE) as estimated by a Doubly Labelled Water experiment; b) Linear relationship of chick (regardless of sex) body mass and DEE.

Observed sex ratio against predictions from Fisher's and Random Assortment

According to *eqn 2* and average DEE values for female and male chicks, the expected sex ratio according to Fisher's equal allocation theory is 0.465, i.e. skewed towards females. However, over the study period the overall pre-fledging sex ratio was on average male-biased (0.523). This observed sex ratio was significantly higher than that predicted by Fisher ($t = 4.42$, $df = 8$, $P = 0.002$), but not from that predicted by random assortment ($t = 1.72$, $df = 8$, $P = 0.124$). However, for the younger chicks, sex ratio was on average female-biased (0.434), and significantly lower than the balanced sex ratio ($t = -3.04$, $df = 6$, $P = 0.023$), but not different from that predicted by Fisher's hypothesis ($t = -1.44$, $df = 6$, $P = 0.201$). On the contrary, for the older chicks the observed sex ratio was on average male-biased (0.606) and deviated significantly from both a balanced ($t = 3.72$, $df = 6$, $P = 0.010$) and Fisher's sex ratio ($t = 4.95$, $df = 6$, $P = 0.003$).

Relationship between environmental covariates and pre-fledgling sex ratio, body condition and sex-differential mortality

The size of the breeding population of glossy ibis between years at the FAO colony was positively correlated with the overall proportion of males ($t = 3.47$, $df = 7$, $r = 0.80$, $P < 0.05$) and with sex-biased mortality ($t = 3.63$, $df = 5$, $r = 0.85$, $P < 0.05$) among pre-fledglings. However, by considering the age groups, we found that with increasing colony size the proportion of males among younger chicks decreased ($t = -2.55$, $df = 5$, $r = -0.75$, $P = 0.05$), while the opposite occurred among older chicks ($t = 1.98$, $df = 5$, $r = 0.66$, $P = 0.10$) (Fig. 2). This difference in sex ratio vs. colony size slopes between age groups was highly significant ($z = 3.22$, $P = 0.001$).

In contrast, the size of the breeding population was negatively correlated with body condition (*females*: $t = -2.96$, $df = 8$, $r = -0.72$, $P <$

0.05; *males*: t = -4.11, df = 8, r = -0.82, *P* < 0.01), with no difference in this effect between sexes (z = 1.31, *P* = 0.19) (Fig. 3).

The surface area of flooded marshes was not related to *overall sex ratio* (t = 1.21, df = 7, r = 0.42, *P* = 0.26), *sex ratio of younger pre-fledglings* (t = 0.14, df = 5, r = 0.06, *P* = 0.89), *sex ratio of older pre-fledglings* (t = 1.98, df = 5, r = 0.25, *P* = 0.58), *sex-biased mortality* (t = 1.22, df = 5, r = 0.48, *P* = 0.27), *female body condition* (t = -1.88, df = 8, r = -0.55, *P* = 0.10) or *male body condition* (t = -1.42, df = 8, r = -0.45, *P* = 0.19).

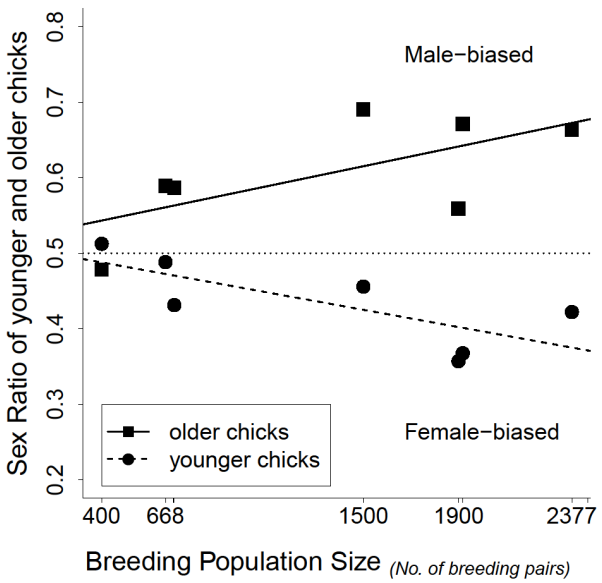

Figure 2. Sex ratios of younger and older chicks plotted against breeding population size. Black circles and the dashed regression line refer to the sex ratio of younger chicks. Black squares and the solid regression line refer to older chicks. The dotted line indicates an even sex ratio.

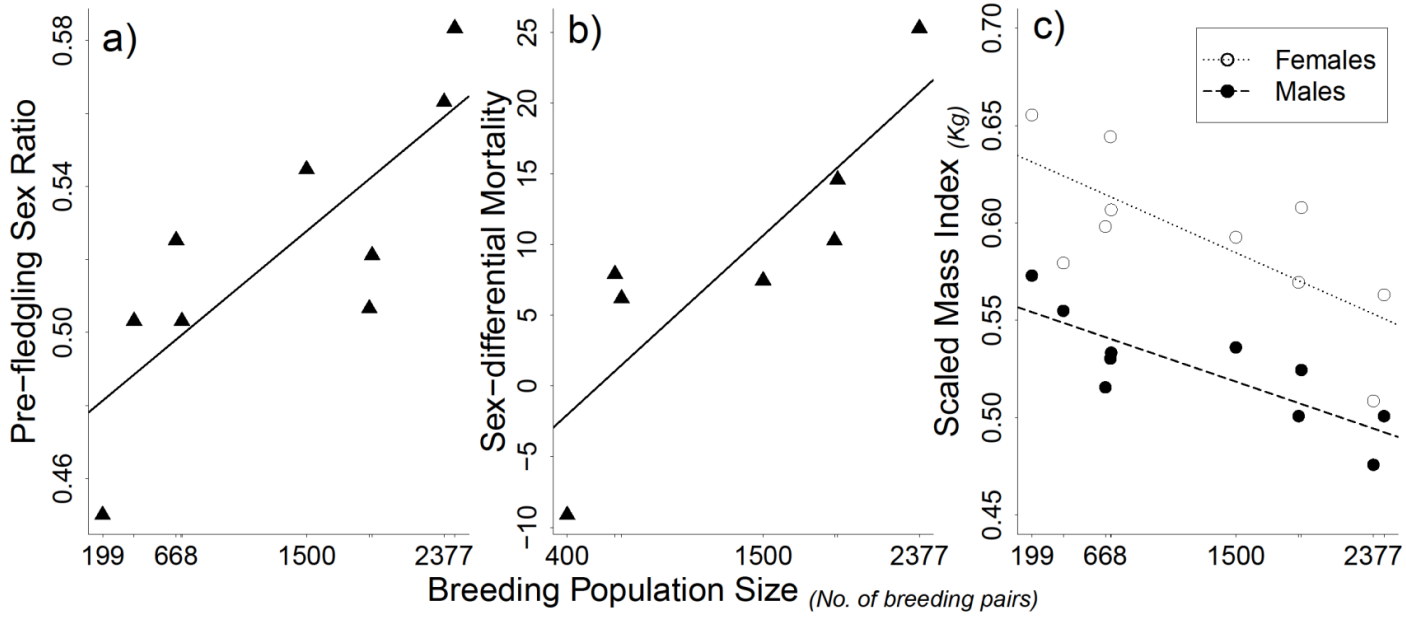

Figure 3. Linear relationships between breeding population size and: a) pre-fledgling sex ratio, b) sex differential mortality and c) body condition. Pre-fledgling sex ratio is estimated as the yearly average sex ratio (proportion of males). Sex differential mortality is proxied by the yearly difference between the average wing length of male and of female chicks. Body condition estimates were calculated as the scaled mass index of mass versus tarsus, separately for females (empty circles) and males (full circles). Regression lines show the relationship between body condition and breeding population size for each sex.

Capítulo II 

Relationship between pre- and post-fledgling sex ratio

We found that an increasing proportion of males among pre-fledglings was associated with a decreasing proportion of males among post-fledglings about four months later ($t = -2.39$, $df = 7$, $r = -0.67$, $P < 0.05$). Although the sample size available was reduced by limiting the test to older pre-fledglings, the effect size of this relationship increased ($t = -3.15$, $df = 5$, $r = -0.82$, $P < 0.05$) (Fig. 4).

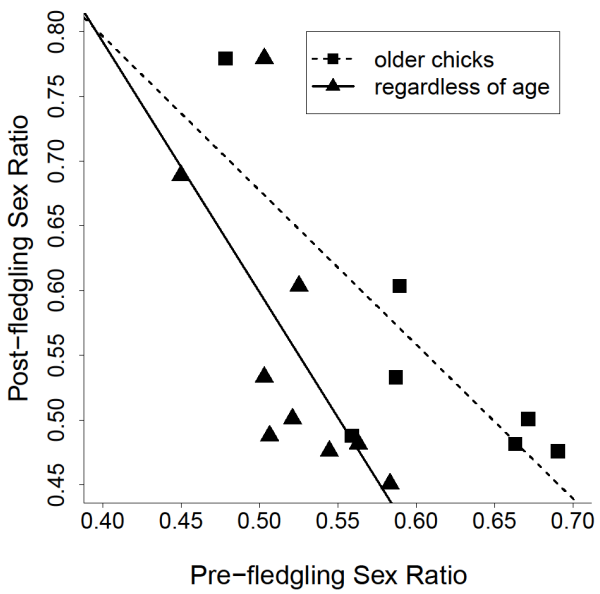

Figure 4. Relationship between pre- and post-fledgling sex ratio (proportion of males). Post-fledgling estimates are from a previous capture-recapture analysis published in Santoro *et al.* (2013) and refer to a few months later (May-July vs. October-December). Both the linear relationship with the sex ratio of pre-fledglings regardless of age (triangles, solid line), and with the sex ratio of older pre-fledglings (squares, dashed line) are shown.

Discussion

By considering younger and older pre-fledglings, we found sex ratio patterns that would have gone undetected had we not accounted for age differences. In particular: *i*) younger pre-fledglings showed a significant female-biased sex ratio, which agreed with the Fisher's prediction and was enhanced by colony size increase, whereas *ii*) older pre-fledglings showed a significant male-biased sex ratio and the effect of colony size was the opposite to that recorded for younger birds. Overall, our findings suggest that poor conditions triggered non-facultative sex-differential mortality, leading to maladaptive fledgling sex ratios which in turn were balanced by sex-related post-fledgling dispersal. Our study suggests the co-existence of facultative and non-facultative adjustments triggered by environmental variation, and affecting life-history traits like body condition, differential mortality and sex ratio.

Pre-fledgling sex ratio

If parents manipulate sex ratio during the parental care period, then Fisher's expectations apply at the time of fledging (discussed in Komdeur 2012). This is coherent with two comparative analyses on birds with sexual size dimorphism, which showed that population-level sex ratios tend to be biased towards the smaller sex at fledging (Pen et al. 2000, Benito and González-Solis 2007). However, in our study the sex ratio close to fledgling showed the opposite pattern.

The observed male-bias in sex ratio at fledging might be adaptive if, as the population increased, the cost/benefit ratio of sons over daughters also increased. Thus, parents might skew the sex ratio by changing the sex-related order (Badyaev *et al.* 2002) or by allocating more to sons than to daughters so enhancing higher mortality rates of the latter. However, none of these mechanisms is supported by our findings. On the contrary, we attribute the sex ratio

observed close to fledging to non-facultative increased mortality of daughters over sons, determined by environmental variation. There are three lines of evidence that support for this hypothesis. First, it could be argued that the change in wing length difference between sexes, which we assumed to be a product of sex-differential mortality, may be explained by an active change by parents of the proportion of males amongst first-hatched offspring. However, this alternative explanation is completely inconsistent with the increasing proportion of females close to hatching observed in relation to density, and the simultaneous opposing pattern close to fledging. Second, if differences in mortality were due to parental decisions allocating more to sons than to daughters, we would have expected a sharper decline in body condition as colony size increased in females than in males. However our data show an identical slope for each sex. Third, if facultative manipulation of sex ratio occurs, it should be towards the same sex both at hatching and fledging (see West 2009; Komdeur 2012), and this was not the case in our study.

In a similar result to ours, Great Tit (*Parus major*) showed a bias towards the larger sex at fledging under poor conditions, which was the opposite of that expected under Fisher's hypothesis (Dhondt & Hochachka (2001). The authors argue that, whereas parents might be able to control primary sex ratio, they could not control the fledgling sex ratio. Thus, a parent-offspring conflict may arise under specific conditions, with the larger offspring sex outcompeting the smaller sex, even though this is detrimental for parents' fitness. Furthermore, the average cost of females would be further reduced because of reduced parental care time devoted to this sex (discussed in West 2009), while the average benefit of males might decrease because poor condition may have a more negative impact on the fitness of the larger sex (Millon et al. 2011). If sex-related mortality occurs regardless of parental manipulation, we should then expect an increasing bias towards females at hatching as environmental

conditions deteriorate. The same outcome would be expected under Fisherian frequency-dependent selection according to which the rare sex has an intrinsically higher reproductive value (Hardy 2002; West 2009). Our study provides strong support for this prediction.

Furthermore, the inverse relationship we found between the fledgling and autumn sex ratios suggests that the excess of males at the end of parental care was counterbalanced by their higher dispersal rate. Our autumn sex ratio estimates originate from a previous capture-recapture analysis (Santoro *et al.* 2013) and refer to the proportion of males among first-resighted individuals, most of which were juveniles. The same pattern would have been observed if members of the majority sex had experienced a higher post-fledgling mortality. However, while it is uneasy to find a sound explanation for the sex- and density-related post-fledgling mortality, it is reasonable to hypothesize that the majority sex dispersed at a higher rate in order to limit intra-sexual competition for mates. This hypothesis is also consistent with the higher recruitment rate of first-year individuals found in another study on this population (Santoro 2014). It is known that the body condition of juveniles is related to their dispersal propensity (e.g. Cristol, Baker & Carbone 1999; Barbraud, Johnson & Bertault 2003). Thus, a possible explanation for our result is that when body condition of both sexes was high (at low population density), females had a higher propensity to disperse than males, whereas when condition was low, the larger size of males conferred a dispersal advantage over females (see also Cristol, Baker & Carbone 1999).

Although we have referred to the effect of breeding population size, this was highly correlated to the elapsed number of years since the colony was first established, which may potentially affect other ecological processes (see e.g. Duckworth & Badyaev 2007) whose effects cannot be separated from those of colony size. Our interpretations rely on an extensive literature linking density-

dependence mechanisms to sex allocation patterns (review in Wilson & Hardy 2002; West 2009).

In this study we suggest that the higher dispersal rate of males was a consequence of non-facultative male-bias in sex ratio at fledging. This is not consistent with the Local Resource Competition hypothesis (Clark 1978, Taylor & Bulmer 1980) according to which the higher dispersal propensity of males would have been a cause of facultative sex ratio biasing. However, it is noteworthy that under both premises the fitness of male offspring and parents would be enhanced as a result of reduced competition among relatives. Furthermore, the suggested relationships between deteriorating environmental conditions and sex-related differential mortality and dispersal pose intriguing questions concerning the role of sex ratio balancing within metapopulation dynamics.

Body condition

Early life body condition is known to affect life-history traits of diverse taxa (Stamps 2006) including waterbirds (e.g. Cézilly et al. 1995; Barbraud et al. 2003). Due to the sexual size dimorphism of this species (Figuerola *et al.* 2006), body condition was estimated separately for each sex. Therefore relative differences in SMI between males and females should not be interpreted as sexual differences in body condition (Fig. 1; see Peig & Green 2009, 2010 for more discussion). The similar decline in body condition over time suggests that poor environmental conditions affected both male and female offspring in a similar manner. Density-dependence effects observed on glossy ibis body condition may have been caused by higher rates of disease or parasite loads (reviewed in Poulin 2011), by increasing sibling competition or by food depletion (Brown and Brown 1996, Tella et al. 2001, Forero et al. 2002, Dann and Norman 2006). The ultimate cause for the decline in body condition, as well as the mechanism responsible for the greater mortality rate in female

chicks, are interesting subjects for future research. However, it would be necessary to focus on the different strategies parents may use when faced with poor conditions and, consequently, study sex ratio at the brood-level. Although the larger sex has greater nutritional requirements, and consequently tends to suffer higher mortality (Clutton-Brock et al. 1985, Bortolotti 1986, Arroyo 2002), the opposite pattern can be true if the larger sex outcompetes the smaller when resources are limited (see also Oddie 2000), as has been suggested for the closely related white ibis (*Eudocimus albus*) (Adams and Frederick 2009). In addition, as found in an experimental study on kestrels (*Falco tinnunculus*) (Fargallo *et al.* 2002), the smaller sex may have lower cell-mediated immunity and therefore higher disease susceptibility under food restriction.

Energetic requirements of female and male chicks

Male glossy ibis chicks had higher energetic requirements than females. When mass was used as a covariate in the analysis, this sex effect disappeared, showing that the sex difference in size caused the difference in energy demands. This dominance of size effects on energy demands of different sexes is consistent with studies of other dimorphic species (Scantlebury et al. 2006). Since the DLW experiment was performed on individuals of various ages, we consider our assumption that the ratio between DEE of males and females is representative of the energetic demand throughout the parental care period to be realistic.

Sampling procedure, a warning for colonial species

Working with colonial species is particularly challenging because of the potential disturbance the fieldwork can cause (e.g. Perennou et al. 1996). When collecting our data we were initially unaware of the biases involved in bleeding. With hindsight, it is perhaps not surprising that a research team may unwittingly select larger

individuals for a more intense handling procedure. A preference for larger individuals is also likely caused by the greater ease of finding the medial metatarsal vein in these individuals. As a result, DNA samples from bleeding provided a distorted sex ratio biased towards males which most likely was caused by a selection towards larger, not necessarily older, individuals. This issue may have been overlooked in previous avian studies in which chicks are sexually dimorphic and form crèches (especially other colonial birds), and caution is required when interpreting any results on sex ratio that come from blood samples in such birds.

Final remarks

Thanks to an intensive monitoring of a newly established breeding colony, we found substantial support for facultative and non-facultative sex ratio adjustment driven by a rapidly changing population size in glossy ibis. In particular, colony size variation triggered a cascade of ecological processes affecting nestling body condition, sex-related mortality and sex ratio. We also found support for autumn natal dispersal as a functional mechanism to regulate the excess of one sex at the end of the parental care period. Since for logistical reasons we could not collect data at the brood-level, we cannot exclude the possibility that other facultative sex ratio adjustments occurred across groups (West 2009). Nonetheless, this study provides a novel example of the way facultative sex ratio adjustments can respond to biological features of the species (e.g. sexual dimorphism), environmental conditions (e.g. population-size) but also to non-facultative sex ratio changes (e.g. sex-differential mortality).

Acknowledgements

This study was funded by projects from the Ministerio de Economia y Competitividad ("Ecología del morito en Doñana: implicaciones para la conservación y gestión del Parque Nacional y su entorno") and Junta de Andalucía ("Las aves acuáticas de Doñana y el cultivo del arroz: la interacción entre la agricultura y la conservación de las zonas humedas"). The collection of samples was possible thanks to El Equipo de Seguimiento de Procesos Naturales (EBD-CSIC). The molecular sexing was performed by Molecular Ecology Lab (LEM). We are especially grateful to L.Garcia, J.L.Arroyo, J.L.del Valle, M.Mañez, F.Ibañez, A.Chico, R.Rodriguez, J.L.Barroso, M.Bauza, M.Pérez, M.Lobon, O.Gonzalez, J.C.González, C.Pérez, C.Moreno, E.García, R.Soriguer, A.Pastoriza, M.Vazquez, and many volunteers that helped with the ringing of glossy ibis chicks.

References

Adams, E. M. and Frederick, P. C. 2009. Sex-Related Mortality of White Ibis (Eudocimus albus) Nestlings During a Starvation Event. - Waterbirds 32: 123–127.

Allainé, D. 1990. The effects of colony size and breeding stage on colony defence pattern in the black-headed gull. - Acta oecologica 12: 385–396.

Anderson, D. J. et al. 1993. Prey Size Influences Female Competitive Dominance in Nestling American Kestrels (Falco sparverius). - Ecology 74: 367–376.

Appleby, B. M. et al. 1997. Does variation of sex ratio enhance reproductive success of offspring in tawny owls (Strix aluco). - Proc. R. Soc. B Biol. Sci. 264: 1111–1116.

Arroyo, B. E. 2002. Fledgling sex ratio variation and future reproduction probability in Montagu's harrier, Circus pygargus. - Behav. Ecol. Sociobiol. 52: 109–116.

Badyaev, A. V et al. 2002. Sex-biased hatching order and adaptive population divergence in a passerine bird. - Science (80-.). 295: 316–8.

Barbraud, C. et al. 2003. Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition. - J. Anim. Ecol. 72: 246–257.

Bates, D. et al. 2012. lme4: Linear mixed-effects models using S4 classes. in press.

Benito, M. M. and González-Solis, J. 2007. Sex ratio, sex specific chick mortality and sexual size dimorphism in birds. - J. Evol. Biol. 20: 1522–1530.

Benowitz-fredericks, Z. and Kitaysky, A. 2005. Benefits and costs of rapid growth in common murre chicks Uria aalge. - J. Avian Biol. 36: 287–294.

Berteaux, D. et al. 1996. Repeatability of daily field metabolic rate in female Meadow Voles (Microtus pennsylvanicus). - Funct. Ecol. 10: 751–759.

Bókony, V. et al. 2012. Multiple indices of body condition reveal no negative effect of urbanization in adult house sparrows. - Landsc. Urban Plan. 104: 75–84.

Bortolotti, G. R. 1986. Influence of Sibling Competition on Nestling Sex Ratios of Sexually Dimorphic Birds. - Am. Nat. 127: 495–507.

Brown, C. R. and Brown, M. B. 1986. Ectoparasitism as a Cost of Coloniality in Cliff Swallows (Hirundo Pyrrhonota). - Ecology 67: 1206–1218.

Brown, M. B. and Brown, C. R. 1996. Coloniality in the cliff swallow: the effect of group size on social behavior. - Chicago University Press.

Brown, C. R. and Brown, M. B. 2001. Avian coloniality. - Curr. Ornithol. Vol. 16: 1.
Butler, P. et al. 2004. Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate methods. - Funct. Ecol. 18: 168–183.
Cézilly, F. et al. 1995. Interannual Variation in Greater Flamingo Breeding Success in Relation to Water Levels. - Ecology 76: 20–26.
Clark, A. B. 1978. Sex ratio and local resource competition in a prosimian primate. - Science (80-.). 201: 163–165.
Clutton-Brock, T. H. et al. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. - Nature: 131–133.
Cohen, J. et al. 2003. Applied multiple regression/correlation analysis for the behavioral sciences. - Lawrence Erlbaum Associates.
Cramp, S. and Simmons, K. E. L. 1977. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic. Vol. I: Ostrich to ducks. - Oxford University Press.
Cristol, D. A. et al. 1999. Differential migration revisited. - Curr. Ornithol. 15: 33–88.
Dann, P. and Norman, F. I. 2006. Population regulation in Little Penguins (Eudyptula minor): the role of intraspecific competition for nesting sites and food during breeding. - Emu 106: 289.
Darwin, C. 1871. The descent of man and selection in relation to sex. (John Murray, Ed.).
Dhondt, A. and Hochachka, W. 2001. Adaptive sex ratios and parent-offspring conflict. - Trends Ecol. Evol. 16: 61–62.
Duckworth, R. A. and Badyaev, A. V 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. - Proc. Natl. Acad. Sci. U. S. A. 104: 15017–22.
Emlen, S. T. et al. 1986. Sex-Ratio Selection in Species with Helpers-At-The-Nest. - Am. Nat. 127: 1–8.
Fargallo, J. A. et al. 2002. Inter-sexual differences in the immune response of Eurasian kestrel nestlings under food shortage. - Ecol. Lett. 5: 95–101.
Figuerola, J. et al. 2006. Sex determination in glossy ibis chicks based on morphological characters. - Ardeola 53: 229–235.
Fisher, R. A. 1930. The Genetical Theory of Natural Selection. - Dover.
Forero, M. G. et al. 2002. Food resource utilisation by the Magellanic penguin evaluated through stable-isotope analysis: segregation by sex and age and influence on offspring quality. - Mar. Ecol. Prog. Ser. 234: 289–299.
Gaston, A. 1985. Development of the young in the Atlantic Alcidae. - In: Nettleship, D. and Birkhead, T. (eds), The Atlantic Alcidae. Academic Press, pp. 319–354.

Götmark, F. 1992. The Effects of Investigator Disturbance on Nesting Birds. - In: Current Ornithology. Springer US, pp. 63–104.
Grafen, A. 1988. On the uses of data on lifetime reproductive success. - In: Clutton-Brock, T. H. (ed), Reproductive success. Studies of individual variation in contrasting breeding systems. University of Chicago Press, pp. 454–471.
Griffiths, R. et al. 1998. A DNA test to sex most birds. - Mol. Biol. 7: 1071–1075.
Guillemain, M. et al. 2013. Individual quality persists between years: individuals retain body condition from one winter to the next in Teal. - J. Ornithol. 154: 1007–1018.
Hamilton, W. D. 1967. Extraordinary sex ratios. - Science (80-.). 156: 477–488.
Hardy, I. C. W. et al. 2002. Sex ratios: concepts and research methods. - Cambridge Univ Pr.
Harvey, M. G. et al. 2006. A comparison of plucked feathers versus blood samples as DNA sources for molecular sexing. - J. F. Ornithol. 77: 136–140.
Komdeur, J. 2012. Sex allocation. - In: Royle, N. J. et al. (eds), The Evolution of Parental Care. Oxford University Press., pp. 171–188.
Król, E. and Speakman, J. 1999. Isotope dilution spaces of mice injected simultaneously with deuterium, tritium and oxygen-18. - J. Exp. Biol. 202: 2839–49.
Kruuk, L. E. et al. 1999. Early determinants of lifetime reproductive success differ between the sexes in red deer. - Proc. R. Soc. B Biol. Sci. 266: 1655–61.
Leigh, E. G. J. 1970. Sex Ratio and Differential Mortality between the Sexes. - Am. Nat. 104: 205–210.
Lessells, C. M. and Avery, M. I. 1987. Sex-Ratio Selection in Species with Helpers at the Nest: Some Extensions of the Repayment Model. - Am. Nat. 129: 610–620.
Magrath, M. J. L. et al. 2007. Estimating expenditure on male and female offspring in a sexually size-dimorphic bird: a comparison of different methods. - J. Anim. Ecol. 76: 1169–1180.
Merino, S. and Potti, J. 1995. Mites and blowflies decrease growth and survival in nestling pied flycatchers. - Oikos 73: 95–103.
Millon, A. and Bretagnolle, V. 2005. Nonlinear and population-specific offspring sex ratios in relation to high variation in prey abundance. - Oikos 108: 535–543.
Millon, A. et al. 2011. Natal conditions alter age-specific reproduction but not survival or senescence in a long-lived bird of prey. - J. Anim. Ecol. 80: 968–75.
Nagy, K. 1983. Doubly labeled water (_3HH_1_8O) method: a guide to its use. - California Univ., Lab. of Biomedical and Environmental Sciences.

Oddie, K. R. 2000. Size matters : competition between male and female great tit offspring. - J. Anim. Ecol. 69: 903–912.
Peig, J. and Green, A. J. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. - OIKOS 118: 1883–1891.
Peig, J. and Green, A. J. 2010. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. - Funct. Ecol. 24: 1323–1332.
Pen, I. et al. 2000. Sex ratios and sex-biased mortality in birds. - In: Pen, I. (ed), Sex allocation in a life history context. PhD thesis. University of Groningen, in press.
Perennou, C. et al. 1996. Management of nest sites for colonial waterbirds. - Conserv. Mediterr. Wetl. No.4. Tour du Valat, Arles. Fr. in press.
Pinheiro, J. et al. 2013. nlme: Linear and Nonlinear Mixed Effects Models. in press.
Poulin, R. 2011. Evolutionary ecology of parasites. - Princeton University Press.
R Development Core Team 2013. R: A Language and Environment for Statistical Computing. in press.
Rendón, M. A. et al. 2008. Status, distribution and long-term changes in the waterbird community wintering in Doñana, south–west Spain. - Biol. Conserv. 141: 1371–1388.
Rózsa, L. et al. 1996. Relationship of host coloniality to the population ecology of avian lice (Insecta: Phtiraptera). - J. Anim. Ecol. 65: 242–248.
Santoro, S. et al. 2010. Formation and growth of a heronry in a managed wetland in Doñana, southwest Spain. - Bird Study 57: 515–524.
Santoro, S. et al. 2013. Environmental Instability as a Motor for Dispersal: A Case Study from a Growing Population of Glossy Ibis (J Faaborg, Ed.). - PLoS One 8: e82983.
Santoro, S. Dynamics and dispersal of a species in expansion, the glossy ibis (*Plegadis falcinellus*). PhD thesis. University of Seville, Spain.
Scantlebury, M. et al. 2006. The energy costs of sexual dimorphism in mole-rats are morphological not behavioural. - Proc. R. Soc. B Biol. Sci. 273: 57–63.
Speakman, J. 1993. How Should We Calculate CO2 Production in Doubly Labelled Water Studies of Animals. - Funct. Ecol. 7: 746–750.
Speakman, J. R. 1997. Doubly Labelled Water: Theory and Practice. - Kluwer Academic Publishers.
Speakman, J. and Racey, P. 1987. The equilibrium concentration of oxygen-18 in body water: Implications for the accuracy of the doubly-labelled water technique and a potential new method of measuring RQ in free-living animals. - J. Theor. Biol. 127: 79–95.

Speakman, J. and Racey, P. 1988. Consequences of non steady-state CO2 production for accuracy of the doubly labelled water technique: the importance of recapture interval. - Comp. Biochem. Physiol. 90A: 337–340.

Speakman, J. and Król, E. 2005. Comparison of different approaches for the calculation of energy expenditure using doubly labeled water in a small mammal. - Physiol. Biochem. Zool. 78: 650–67.

Speakman, J. et al. 1990. Interlaboratory comparison of different analytical techniques for the determination of oxygen-18 abundance. - Anal. Chem. 62: 703–708.

Speakman, J. et al. 1994. Inter- and intraindividual variation in daily energy expenditure of the pouched mouse (Saccostomus campestris). - Funct. Ecol. 8: 336–342.

Stamps, J. A. 1990. When Should Avian Parents Differentially Provision Sons and Daughters ? - Am. Nat. 135: 671–685.

Stamps, J. A. 2006. The silver spoon effect and habitat selection by natal dispersers. - Ecol. Lett. 9: 1179–85.

Taylor, P. D. and Bulmer, M. G. 1980. Local mate competition and the sex ratio. - J. Theor. Biol. 86: 409–419.

Tella, J. L. et al. 2001. Offspring body condition and immunocompetence are negatively affected by high breeding densities in a colonial seabird: a multiscale approach. - Proc. Biol. Sci. 268: 1455–61.

Torres, R. and Drummond, H. 1999. Does large size make daughters of the blue-footed booby more expensive than sons? - J. Anim. Ecol. 68: 1133–1141.

Trivers, R. L. and Willard, D. E. 1973. Natural Selection of Parental Ability to Vary the Sex Ratio of Offspring. 179: 90–92.

Trivers, R. L. and Hare, H. 1976. Haploidploidy and the evolution of the social insect. - Science (80-.). 191: 249–263.

Van de Pol, M. et al. 2006. A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (Haematopus ostralegus). - J. Anim. Ecol. 75: 616–26.

Van Trigt, R. et al. 2002. Validation of the DLW method in Japanese quail at different water fluxes using laser and IRMS. - J. Appl. Physiol. 93: 2147–54.

Visser, G. H. and Schekkerman, H. 1999. Validation of the doubly labeled water method in growing precocial birds: the importance of assumptions concerning evaporative water loss. - Physiol. Biochem. Zool.: 740–749.

Ward, P. and Zahavi, A. 1973. The importance of certain assemblages of birds as "information-centres" for food-finding. - Ibis (Lond. 1859). 115: 517–534.

West, S. A. 2009. Sex allocation. - Princeton Univ Pr.

Wiebe, K. L. and Bortolotti, G. R. 1992. Facultative sex ratio manipulation in American kestrels. - Behav. Ecol. Sociobiol. 30: 379–386.

Wilkin, T. A. and Sheldon, B. C. 2009. Sex Differences in the Persistence of Natal Environmental Effects on Life Histories. - Curr. Biol. 19: 1998–2002.

Wilson, K. and Hardy, I. C. W. 2002. Statistical analysis of sex ratios: an introduction. - Sex ratios concepts Res. methods: 48–92.

Appendix 1 - Body Condition calculation

We calculated an index of body condition by using the method proposed by Peig & Green [1]. This method consists of calculating a Scaled Mass Index (SMI) as follow:

$$\hat{M}_i = M_i\left[\frac{L_0}{L_i}\right]^{b_S} \qquad \text{(eqn 1)}$$

where, for each sex separately, Mi and Li represent the i-individual measures of mass and a length measurement (we used tarsus), L0 is a standardized length measure (we used the arithmetic mean of tarsus) and bSMA is the scaling exponent given by the log-log regression of mass on the length measurement (tarsus, calculated by an online software [2]). As recommended in Peig & Green [1] we chose tarsus as the morphometric variable because it has the strongest correlation with the mass on a log scale. Then, represents the predicted body mass of the ith-individual when the tarsus length is standardized to L0. In our case, L0 was 95.36 mm for males and 82.33 mm for females.

References

Bohonak, A. J. and van der Linde, K. 2004. RMA: software for reduced major axis regression, Java version./<www.kimvdlinde.com/professional/rma.html/>

Peig J and Green AJ (2009) New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. OIKOS 118: 1883–1891

Capítulo 3

Immigration enhances fast growth of a newly-established source population

Simone Santoro[1], Andy J. Green[1], and Jordi Figuerola[1]
1 Department of Wetland Ecology, Doñana Biological Station-CSIC, Avda. Américo Vespucio s/n, 41092, Seville, Spain

Short title: Immigration and local recruitment of spreading glossy ibis

Santoro, S., Green, A. J. & Figuerola, J. (submitted to Journal of Animal Ecology). Immigration enhances fast growth of a newly-established source population

Summary

1. Immigration and local recruitment play a crucial role in determining the growth rate of populations. Unraveling this process in newly-established populations is of primary importance, especially under global change scenarios which predict redistribution of species.

2. We studied the biggest colony of glossy ibis (*Plegadis falcinellus*) in Western Europe (established in Doñana, SW-Spain since 1996) by using capture-recapture methods, count estimates and projection matrix modeling to: (*i*) test the effect of resources availability and competition on local recruitment dynamics, (*ii*) investigate the contribution of local recruitment vs. immigration on population growth, and (*iii*) assess the role of this population in source/sink dynamics.

3. We found different dynamics before and after the establishment of other Doñana colonies in 2004. Between 1996 and 2003, the colony size increased rapidly, fuelled by influx of immigrants (≈ 58 breeding females/year). However, between 2003 and 2007, both population increase and immigration were negligible. Immigration played a major role in colony growth, but simultaneously Doñana was a source for species expansion as suggested by (*i*) absolute and relative estimates of the observed growth rate and that predicted by self-recruitment, and (*ii*) by numerous observations of Doñana-born individuals breeding elsewhere. Local recruitment was unrelated to resource availability, previous-year breeding failure and competition. However, local recruitment, that was particularly high for first-year individuals (>0.8 over the first period), decreased rapidly at a certain population size when other satellite colonies became established at Doñana.

4. Our findings reveal that, as well as early recruitment and high productivity, immigration may play a pivotal role promoting the

fast growth of new populations, at least until density-dependent effects arise. This process can be so fast that a new population can become itself a source population driving range expansion of the species in a matter of a few years.

Introduction

The distribution of many species of birds and other organisms is undergoing rapid change in response to the effects of human activities on habitats and food supply, as well as climate change [1]. These changes in distribution reflect processes going on at the level of individuals and populations that are usually poorly understood and hard to study. In most organisms, the counting of population size and tracking of individuals is impractical. However, in the case of colonial birds that can be marked individually with rings, much can be learned about the population processes and how they relate to changing distribution. For example, in expanding species, do newly-established colonies on the edge of the range act as independent units that build up in size and only export individuals to create more colonies once a carrying capacity threshold is reached? Or do they contribute to the creation of further colonies from the beginning? Does their establishment require the continued arrival of immigrants from elsewhere, or is this only required in the first few years? In this study we address these questions in the case of the glossy ibis, one of various colonial waterbird species that are currently undergoing expansion across parts of Europe.

Environment and genetic constraints regulate life-history traits and ultimately population size [2–4] mostly by variation in (*i*) survival, (*ii*) age at first reproduction, and (*iii*) number of fledglings per pair. If estimates of these parameters are available, they can be used in matrix models [5] to estimate the contribution of local recruitment to the population growth (e.g. [6]) which, in turn, depends also on immigration/emigration. Within a metapopulation [7], the recruitment and growth rates of a specific population determine its source-sink dynamic and therefore greatly affect metapopulation dynamics and species distribution. This is clearly outlined by Peery and colleagues [8] who focusing uniquely on

recruitment and growth rates provide straightforward criteria to find out if a local population is sustaining other populations with new individuals (i.e. source) or if its own persistence depends on immigration (i.e. sink).

Dispersal provides a rapid and efficient response to abrupt environmental changes (e.g. [9,10]) affecting both the populations growth rate and the geographical distribution of species [1,11]. However, other demographic parameters like survival or reproduction relate to environmental and population changes. It is then of primary importance investigating the mechanisms relating environment to life-history and ultimately population dynamics variation in particular at the range limits where peripheral populations may be promoting the geographical expansion of the species [12].

The rate at which new breeders recruit can be affected by several biotic, abiotic, intrinsic, and extrinsic factors. For instance, the 'conspecific attraction hypothesis' [13,14] posits that local population size can be used by potential recruits as a proxy for environmental conditions and therefore affect their settlement decision. Within the body of empirical support to this hypothesis, Oro and Pradel [15] found a clear positive relationship between colony size and local recruitment in a growing population of Audouin's gulls (*Larus audouinii*). Also, more than the mere presence of conspecifics, their reproductive success can be used to assess the suitability of a site for recruiting [16] as evidenced by several studies on diverse bird species (e.g. [17–19]). A number of other factors, related to the extent of competition like food availability or mass at fledging have been found to relate to recruitment [20–22]. The age at first reproduction is especially relevant for the breeding population growth. Life-history theory posits that the optimal age at first reproduction depends on the trade-off between benefits and costs of early reproduction in terms of survival and future reproduction [2]. Since survival and reproductive performance tend to increase with

age [23], the specific extent of this relationship has a crucial effect on the optimal age at first reproduction. A number of non-exclusive hypotheses have been proposed to explain why age should positively relate to the reproductive performance (differential survival, reproductive effort, breeding experience, etc.) [23]. However, while there is a consensus on a common positive relationship between longevity and age at first reproduction (e.g. [24]), other factors, like habitat heterogeneity and population density (e.g. [25]), might break this general rule by adding further complexity to the life-cycle.

The glossy ibis is a worldwide spread long-lived bird species [26] whose population dynamics has received little attention ([9,27] and references therein) and with scarce information on their main demographic parameters (but see [28–31]). The Doñana population established in 1996 [32,33] from seven breeding pairs and showed a steep increase until present ([32,33] and unpublished data). It has been proposed that this population has played, and still plays, a crucial role for the undergoing range expansion of the species across the Mediterranean basin and Western Europe [9,27].

In this study, we aimed to investigate the demographic process beyond the expansion of a species by focusing on long-term data collection from a large population of glossy ibis settled at Doñana. In particular, we: (*i*) evaluated hypotheses on the local survival and recruitment process by considering the effects of age, sex, availability of resources or breeding sites, population size, breeding success, and extreme events; (*ii*) investigated the source-sink nature of the studied population while assessing how its dynamic depended on local recruitment and immigration; and (*iii*) described the range expansion involving Doñana-born marked individuals.

Methods

Study Area, Field Data

Doñana is a vast protected wetland area in SW Spain covering about 108,087 ha (details in [32,34]). In 1996 seven breeding pairs of glossy ibis settled at Doñana in a 50 ha restored semi-artificial pond-system named "Lucio de la FAO" (FAO hereon) [9,32] after being locally extinct from historical times [27]. The population showed a strong population growth with more than 7,000 breeding pairs estimated in 2011 at Doñana. After a first period (1996 - 2003) when they only bred at the FAO colony, they started to breed also in other Doñana sites. Over the last twenty years, smaller breeding colonies have been established in East and North-East Spain (respectively 1993 and 1996; [33]), in Camargue (Southern France, 2006; [35]), Argelia (1998; [36,37]), South-West and North Morocco (respectively 1994 and 2011; [37,38]). Additionally, irregular and often unreported in literature breeding has occurred in several countries like Portugal [39], Italy [40,41], and some other areas in Spain, France [42] and Morocco, especially since the lack of reproduction in 2005 due to a severe drought in Doñana ([9]; details in Table S1, Supporting Information).

Since the settlement at Doñana more than 16,000 chicks have been marked with darvic rings with an individual alphanumeric code (3 - 4 digits) easy to be read with a telescope from a distance of up to 100 meters. Almost 4,000 chicks have been unequivocally sexed by DNA [43]. Furthermore, regardless of molecular sex determination, from 1998 onward ca. 10,000 have been visually sexed according to tarsus shape [44], with an error probability (range 0.01 - 0.2) which depended on year and ringer (see [9] for more details). Both breeding population size and productivity (no. of fledglings per pair) have been yearly assessed by visual census (details in [33]).

Analytical approach

Our approach integrates capture-recapture (CR) estimates of local demographic parameters, counts, matrix population modeling [45] and observations of Doñana-born individuals outside their natal site. Firstly, we used CR modeling to test hypotheses on intrinsic and extrinsic factors regulating local survival and recruitment. Secondly, we used CR and count estimates within matrix models to assess the contribution of local recruitment vs. immigration and therefore the source-sink role of the studied population. Thirdly, we performed a sensitivity analysis to determine the importance of each intrinsic parameter (survival, recruitment, and productivity) on population growth. Lastly, we described the range expansion throughout the study period from observations of marked individuals born at Doñana.

Survival and Recruitment analysis

We performed a multi-event CR analysis [46] to test hypotheses on the local survival and local recruitment by using resightings of individuals (n = 5565) at the FAO colony during the breeding season (April - July) between 1996-2007. Observations at the breeding colony after 2007 were sparse and were therefore excluded by the analyses. The individuals' access to the colony was used as a proxy for recruitment whose estimates may be biased if non-breeders visited regularly the colony. However, our observations suggest that this is not the case as several resighted juveniles and adults were recorded in breeding activity and no evidence of helpers at nest exists in this species [29]. The multi-event approach ([46]; details in Appendix S1) aimed to deal with uncertainty on sex determination of glossy ibis chicks by accounting for sex identification by both DNA- and visual sexing. In this study we considered five biological states: † - death or permanently emigrated, ♀NB - alive female non-breeder, ♀B - alive female breeder, ♂NB - alive male non-breeder, and ♂B - alive male breeder. We assumed once an individual

became a breeder it was forever and considered two age classes both for local survival and recruitment rate (Fig. 1). These states were mediated by four events, numbered as they appear in the encounter histories: (0) not seen, (1) seen visually sexed as a female, (2) seen visually sexed as a male, (3) seen visually unsexed. Five parameters were estimated (names in capitals): (*i*) Initial State, the probability a marked individual had of being a female chick when ringed at time *t*; (*ii*) Survival, *p* of surviving and do not emigrating permanently between *t* and *t* + 1; (*iii*) Recruitment, conditional on Survival, *p* of recruiting between *t* and *t* + 1; (*iv*) Resighting, *p* of being resighted at time *t* + 1; (*v*) Visual Sexing, conditional on Resighting, *p* of being visually sexed when first captured and marked; and (*vi*) Correctness, conditional on Visual Sexing, *p* that visual sex was correct. Models were run in E-SURGE (version 1.8.5) [47].

We used U-CARE (version 2.3.2) [48] to perform a goodness-of-fit test of the general Cormack-Jolly-Seber model on all observations of marked individuals (but first capture) and found no significant lack of fit (Global Test: $\chi_{[5]} = 21.6$, $p = 0.86$). We considered an age effect (two age classes) on Survival to account for differences in this parameter between chicks and adults.

Parameter types were modeled separately into sequential steps to limit both the bias from the modeling order and the number of models (Appendix S1; see [9,49] for analogous procedure). Accordingly to previous analyses [9] both Visual Sexing and Correctness were held as depending on cohort. As a general rule, throughout the model simplification process we retained the structure of models whose AIC_c (Akaike Information Criterion corrected for small sample sizes) was at least 2 units lower than others or, in case others existed within 2 AICc units, the least parameterized was retained [50]. Due to data sparseness we set Survival constant over time and tested only for variation by sex and breeding status. In the final step, we evaluated the effect on Recruitment of: (*i*) breeding

success at time *t*, (*ii*) flooded marsh surface at time *t* and *t* + 1, (*iii*) population size at the FAO colony, (*iv*) dry vs. non-dry years and, (*v-vi*) time and cohort effects before and after the settlement of other breeding sites at Doñana. We used the ANODEV procedure to test the effect of each covariate by comparing the deviance of the null, full time-dependent and covariate model; furthermore, we estimated the extent of each covariate effect as the amount of deviance explained [51].

Ninety-five confidence intervals of boundary estimates was calculated by the profile likelihood method since the default Wald method is inappropriate in these cases [52]. Thus, we iteratively fixed that parameter to decreasing (if close to 1) or increasing (if close to 0) values until the model deviance changed significantly (which corresponds to a change of 3.84 in deviance, see [53]).

Local recruitment and immigration contribution to the population growth

Based on CR analyses suggesting local recruitment mostly varied between two periods, before and after the creation of Doñana colonies satellite to the FAO colony: 1996-2003 (only FAO) and 2003-2007 (FAO plus others).

Firstly, for each period we calculated the observed average breeding population growth rate and its 95% CI by performing a regression of $\log(N_{i+1}/N_i)$ onto $\sqrt{year_{i+1}/year}$ where N_i are the number of pairs counted in the *i*-year (details in [54]; see also Appendix S2). Secondly, for each period we calculated the predicted growth rate, as the dominant eigenvalue (R package *popbio*; [55]) of the Leslie projection matrix built with estimates of local survival, local recruitment and productivity ([6,56]; see next section). As population size and number of fledglings increased estimates of productivity became less reliable [33]. Therefore, we considered a single value for the entire study period that was obtained by data collected over the first period. According to CR model selection we considered two age classes (first-year vs. others) for both survival and recruitment rates and, for the second age class, a different survival rate for non-breeder and breeder individuals. Capture-recapture estimates were obtained from a model (model R7 in Table 1) with the same variables as the best one except for considering a two-periods (1996-2003 and 2003-2007) time-effect on local recruitment. Although this was at the cost of loosing some realism, it allowed us to maintain a simple and logical framework to test the population dynamics over these two periods that, as indicated by CR model selection, were strikingly different. We defined a female-based time-invariant matrix model that considered the following stages: newborn individuals, non-breeder first-year individuals, non-breeder adults (>1 year old), breeder first-year individuals and breeder adults. As for CR analyses, we assumed that once an individual became a breeder it remained

breeder for the rest of its life (Fig. 1). Thus, the Leslie matrix was defined as:

$$\begin{matrix} \varphi_1 * \psi_1 * f * 0.5 & \varphi_{2-NB} * \psi_2 * f * 0.5 & \varphi_{2-NB} * \psi_2 * f * 0.5 & \varphi_{2-B} * f * 0.5 & \varphi_{2-B} * f * 0.5 \\ \varphi_1 * (1-\psi_1) & 0 & 0 & 0 & 0 \\ 0 & \varphi_{2-NB} * (1-\psi_2) & \varphi_{2-NB} * (1-\psi_2) & 0 & 0 \\ \varphi_1 * \psi_1 & 0 & 0 & 0 & 0 \\ 0 & \varphi_{2-NB} * \psi_2 & \varphi_{2-NB} * \psi_2 & \varphi_{2-B} & \varphi_{2-B} \end{matrix}$$

where φ refers to the local survival rate, ψ to the recruitment rate, *f* to the fecundity (productivity) and the subscripts '1', '*2*', '*NB*', and '*B*' respectively to the first vs. other years of life, non-breeder and breeder.

While the predicted growth rate depends uniquely on self-sustained growth, the observed depends also on immigration (see Appendix S2). As indicated by Peery et al. [8], we investigated the source/sink nature of the study population by testing if count-derived and matrix-predicted growth rates were different from 1 (stable population) and from each other. In case the observed growth rate was significantly higher than the matrix-predicted, we included in the Leslie projection matrix another stage, immigrants [6,57], and iteratively repeated (*n* = 10,000; see next section) the process to calculate the annual average number of female immigrants needed to match the observed population size at the end of each period.

Simulations and Sensitivity

For each study period (1996-2003, 2003-2007) we used Latin Hypercube Sampling (R package *lhs*, [58]) to create 10,000 simulations consisting each one of a random set with realistic ranges (95%CI estimates) of the demographic parameters used in the Leslie matrix. Apart from estimating the predicted growth rate and number of immigrants, these simulations were used to perform a sensitivity analysis (R package *sensitivity*, [59]) aimed to determine the importance of each intrinsic demographic parameter (productivity,

age-specific local survival and recruitment) on the predicted growth rate. Details on matrix modeling and simulations are given in Appendix S2.

Breeding dispersal of Doñana-born individuals

We described the spatial distribution of resightings of Doñana-born individuals dispersing elsewhere over the last 19 breeding seasons. We only considered resightings more than 100 Km apart from Doñana and grouped them separately according to whether or not the individual was recorded as a breeder. With the objective of focusing on breeding dispersal, we only considered resightings during the core breeding period (May-July), except for individuals reported as breeders.

Results

Local survival and recruitment

Model selection results are summarized in Table 1 and Table S2 (Supporting Information). Resighting probabilities varied through the study period (Fig. S1, Supporting Information). Initial State (i.e. the probability a chick was marked being a female) remained constant across the study period (0.53, 95%CI 0.49 - 0.57).

Local survival of juveniles (0.75, 95%CI 0.65 - 0.83) did not differ between sexes but it was different from that of adults, which in turn depended on sex and breeding state (models S-2 Table S2). Among adult males, local survival probability appeared to be much higher for breeders (0.85, 95%CI 0.81 - 0.89) than for non-breeders (0.01, 95%CI 0 - 0.68). On the contrary, among adult females, breeders had lower survival rates compared to non-breeders who in turn showed the highest probability of surviving and not leaving the study area (breeder: 0.73, 95%CI 0.68 - 0.78; non-breeeder: 0.99, 95%CI 0.78 - 1).

The additive effect of age, sex and a specific combination of cohorts explained about 92% ($F_{1,7}$ = 6.39, P < 0.05) of local recruitment time-variation (model R1 in Table 1). On average, the probability of recruiting was much higher for first-year individuals than adults and slightly higher for males than females (Fig. 2). Also, recruitment probability was higher and constant for cohorts born before 2003, but progressively declined for the subsequent cohorts (Fig. 2). Notably, before the establishment of additional colonies (in 2004) which occurred at a population size of about 700 breeding pairs, the local recruitment probability was constant for both first-year males (0.87, 95%CI: 0.74 - 0.94) and first-year females (0.78, 95%CI: 0.64 - 0.87). A model accounting for an analogous time (instead of cohort) effect on recruitment rate was similarly supported by data (model R2 in Table 1, ΔAIC_c = 1.60). Breeding success,

population size, flooded marsh surface, or dry years had no effect on local recruitment (Table 1).

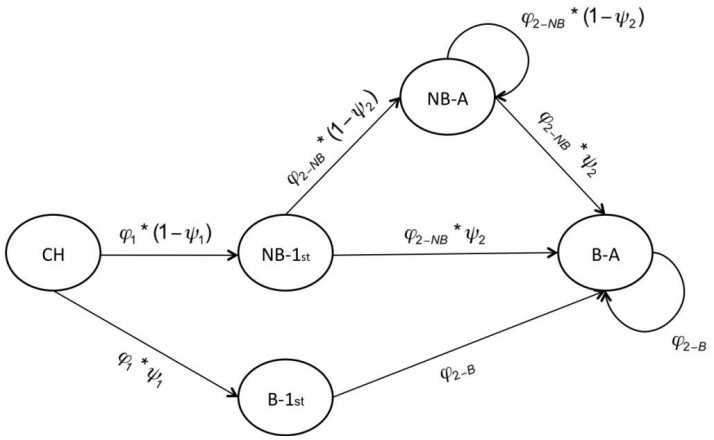

Figure 1. Probabilistic diagram of glossy ibis life-cycle. State-transitions between *t* and *t* + 1 regardless of sex. Notation: *CH*, chick; *NB-1st*, first-year non-breeder juvenile; *NB-A*, adult non-breeder; *B-A*, adult breeder; *B-1st*, first-year breeder; φ, local survival probability; ψ, local recruitment probability; subscripts $_1$ and $_2$ refer respectively to probability specific for age 1 (first year of life) and age 2 (older ages), subscripts $_{NB}$ and $_B$ respectively to non-breeder and breeder. Transitions towards dead or permanently emigrated state are not explicitly represented.

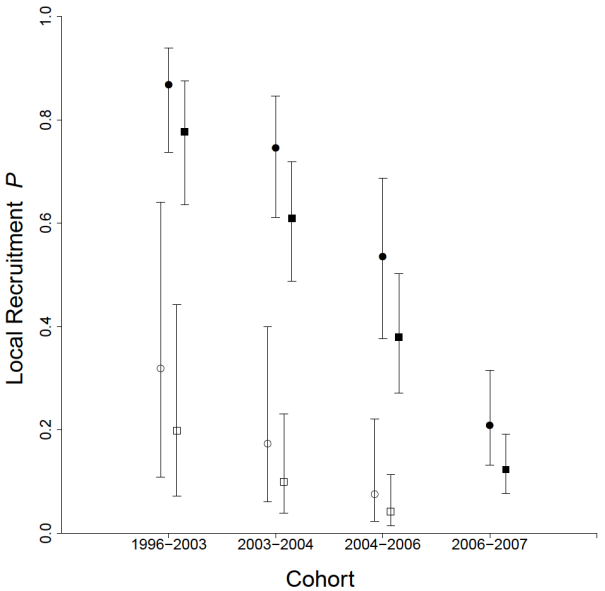

Figure 2. Local Recruitment. Mean and ninety-five CI local recruitment estimates obtained from the lowest AIC_c model accounting for the effect of age, sex and cohort. According to this model the local recruitment probability over the first period (1996-2003) is constant. Notation: filled circles refer to juvenile males, filled squares to juvenile females, empty circles to adult males, empty squares to adult females.

Observed population growth rate

The annual average growth rate of the FAO population was significantly larger than one ($\lambda_{obs\text{-}1}$ = 1.92, 95%CI 1.45 - 2.38, Z = 3.85, $P_{two\text{-}tailed}$ < 0.001) through the first period (1996-2003) when recruitment at Doñana was possible only at the FAO colony, but was lower and non-significantly different from one since them ($\lambda_{obs\text{-}2}$ = 1.22, 95%CI 0.80 - 1.87, Z = 1.04, $P_{two\text{-}tailed}$ = 0.30).

Contribution of local recruitment and immigration to the population growth rate

The annual average number of fledglings per pairs as estimated by counts made over the first period was 2.12 (95%CI 1.38 - 2.86). According to the matrix model (i.e. without immigration influx), the predicted annual growth rate would have been positive for the first period ($\lambda_{pred\text{-}1}$ = 1.43, 95%CI 1.21 - 1.66, Z = 3.79, $P_{two\text{-}tailed}$ < 0.001), and non-significantly positive during the second period ($\lambda_{pred\text{-}2}$ = 1.26, 95%CI 1.10 - 1.43, Z = 1.43, $P_{two\text{-}tailed}$ = 0.15) (Fig. 3).

We found that over the first study period the observed annual growth rate exceeded that predicted by matrix model (Z = 5.36, $P_{one\text{-}tailed}$ < 0.001) indicating a net immigrant influx that we estimated at 58 female immigrants on annual basis (95% CI 35 - 92). Over the second period the observed growth rate was not significantly different than the matrix-predicted (Z = -0.38, $P_{two\text{-}tailed}$ = 0.71) meaning that no net immigration occurred.

According to the criteria detailed in Table S3 (Supporting Information), the FAO population could be categorized as "open and a potential source" during the first period (1996 – 2002) and "closed, or a source" throughout the second period (2003 – 2007).

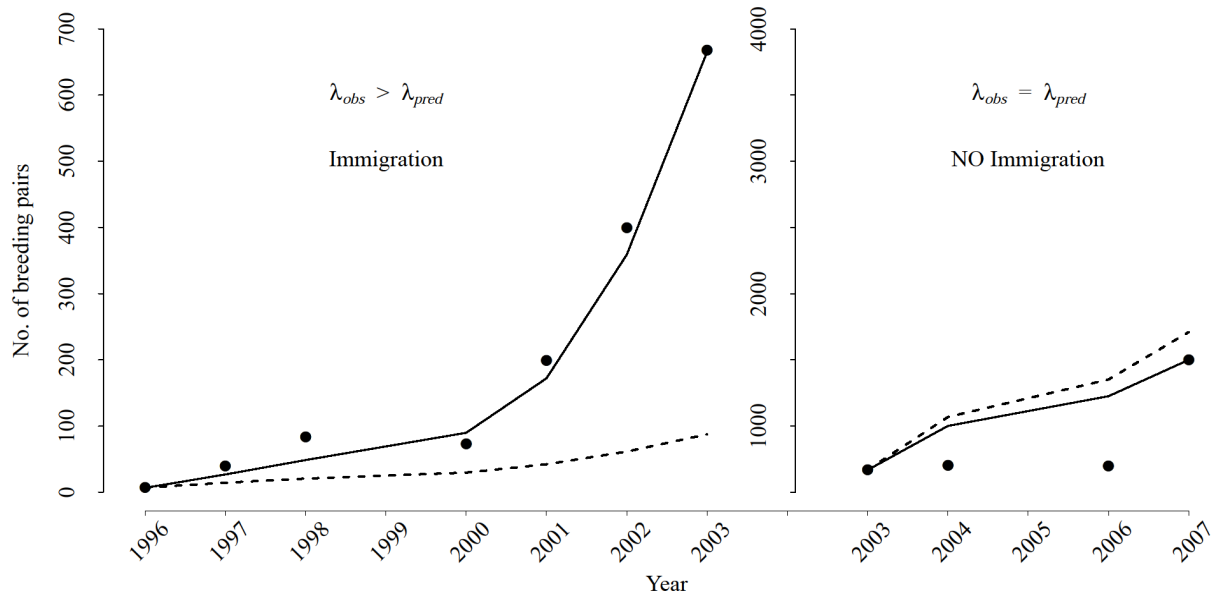

Figure 3. Population growth rate. The population trend observed and predicted by projection matrix modeling (without immigration) over the first period (1996 - 2003) when only a breeding site existed at Doñana and over the second period (2003 - 2007) when other colonies appeared. Notation: filled circles, count estimates; filled line, the trend line fitting the count estimates; dashed line, matrix-model predicted growth line. λ_{obs} and λ_{pred} refer respectively to the annual average finite growth rate (N_{t+1} / N_t) calculated by count estimates and matrix modeling.

Sensitivity analysis

The number of fledglings per pair had the greatest potential impact on the predicted population growth rate (Fig. S2, Supporting Information). We found that without any contribution from immigration and keeping the other demographic parameters unchanged, 3.85 fledglings per pair (ca. 1.8 times the realized value) would have been needed to achieve the observed growth rate through the first period.

Breeding dispersal distribution area

Three hundred and forty-nine Doñana-born marked individuals have been resighted elsewhere during the breeding seasons along the study period: 61 of them were reported as active breeders. The first record occurred in 1999 concomitant with the first Doñana dry year during the study period, but the subsequent resighting was not until the next local drought (in 2005) when the ibis did not breed in Doñana (Table S1). The observations depict an area stretching from South-west Morocco to Scotland to the western shore of the Black Sea (Fig. 4). A Doñana-born individual was seen in July 2008 in Trinidad y Tobago and another in September 2010 in Barbados.

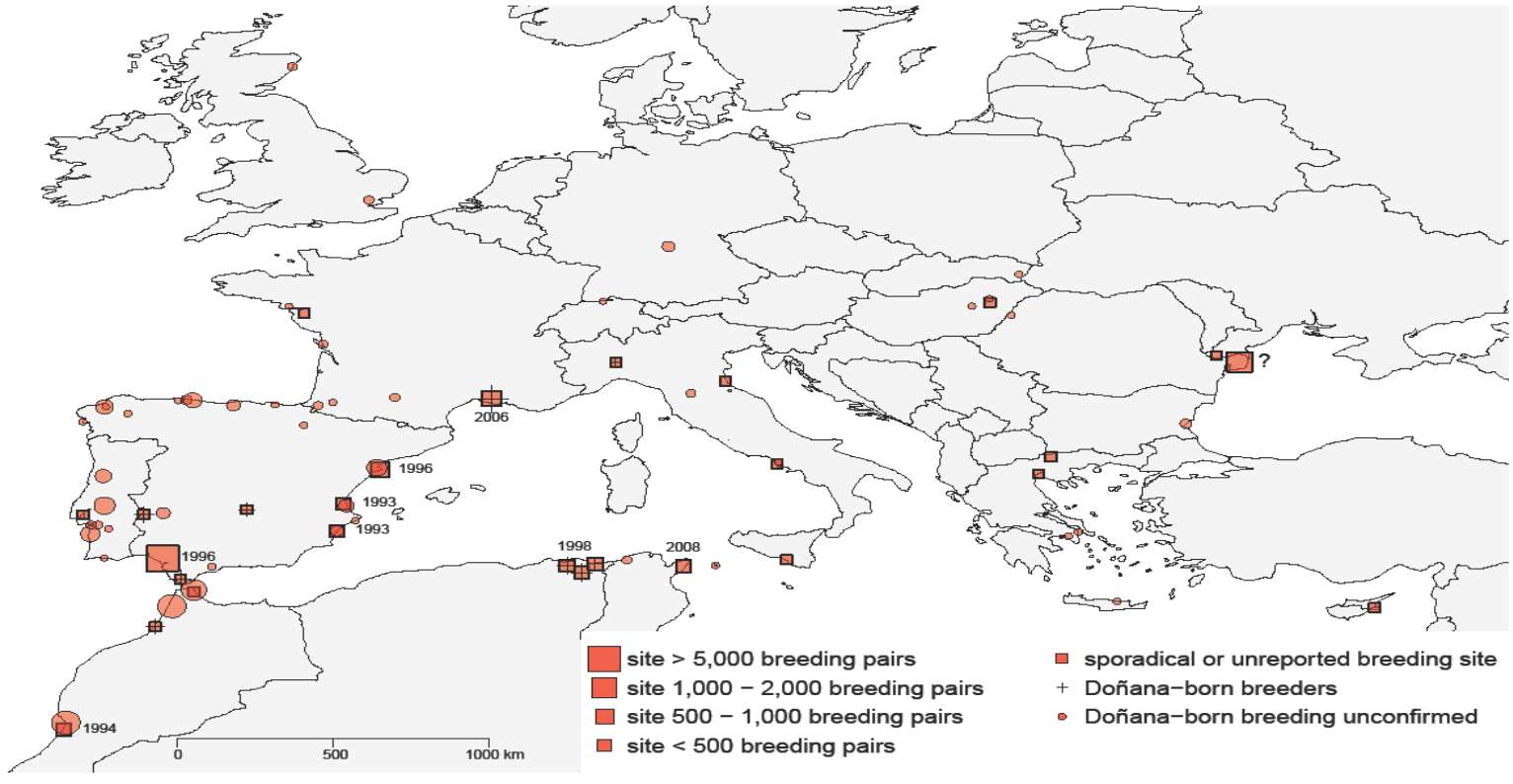

Figure 4. Map of resightings. Observations of Doñana-born marked individuals more than 100 Km apart from their natal colony during the breeding time (May – July). A distinction is made between individuals for which breeding activity has been informed by resighter (cross symbol) and individuals for whom no information on breeding activity is reported (full circle symbol). Observations of two individuals in Central America (see text for details) are not reported for scaling reasons. The location of a number of known breeding areas is reported (square symbol) and the year of formation of the colony is indicated when known; the size of breeding location symbol is proportional to the number of breeding pairs in recent years. The smallest square symbol refers to a non-exhaustive record of occasional or unreported in scientific literature breeding sites. Most likely other unknown breeding sites of glossy ibis exist in the map area.

Discussion

Our study shows that a new waterbird colony can experience a sharp increase largely due to immigration at least until density-dependent mechanisms arise. As well as immigration, high productivity and early recruitment may enhance the creation of a new source population crucial for the expansion of the species. Furthermore, our findings suggest that if males failed at recruiting as juveniles, they had a much higher probability of permanently emigrating than had females. Males and females may therefore follow quite different strategies depending on interactions between environmental and demographic factors.

According to the 'attraction hypothesis' [13] and the 'conspecific reproductive success hypothesis' [16], potential recruiters might rely respectively on population size and breeding success as a proxy for environmental conditions [13–15] therefore affecting local recruitment rates. Nonetheless, neither breeding success nor colony size related to local recruitment. As a possible explanation, using public information (sensu Valone 1989 [60]) may be favored when the environment is predictable [61]; conversely, Doñana provides good-quality but highly variable conditions for a number of colonial species which have also increased their breeding populations in the area during the study period (see [62]). As supported by the strong cohort effect we found, density-dependent mechanisms may have been masked by the formation of new, neighboring colonies within Doñana where many FAO native individuals might recruit with negligible dispersal-related costs. Neither the effect on local recruitment of flooded marshes surface nor that of dry years was supported. However, we cannot exclude that availability of resources had an effect on local recruitment since the extent of flooded marshes might be a too naïve approximation to test this hypothesis (see [9] for a discussion on this). On the other hand, a previous CR analysis of

post-breeding longitudinal data indicated that dry years at Doñana strongly enhanced permanent emigration of native individuals [9]. The present study confirms this pattern; in fact, while the first observation of a Doñana-born individual elsewhere coincided with the first dry year (1999), it was not until the next one (2005) when other individuals were seen dispersing. However, if dry years had negatively affected the local recruitment rate, we might have overlooked that circumstance because of the concurrent local recruitment decrease started after the formation in 2004 (just before the second dry year) of satellite colonies. A basic assumption of our modeling approach is that individuals remain breeding every year after their first recruitment. However, in long-lived birds individuals may skip breeding when conditions for reproduction are not good. Temporary emigration biases transition estimates if it is Markovian (i.e. depending on breeding status at the previous occasion), but it does not if it is random [63]. However, this point should not be of concern since the test 2.CT (from goodness-of-fit analysis) [48], which has good power to detect Markovian temporary emigration, resulted non-significant.

Also, our findings suggest that males unable to breed at their first year of life were much more prone to disperse than females. Notably, previous studies on the sex ratio and dispersal in the same population [9,64] suggested that: (*i*) along with increasing density-dependent competition, more female than male chicks died during the parental care period, gradually biasing the fledging sex ratio towards males; (*ii*) the opposite temporal pattern appeared among the post-fledging sex ratio suggesting that sex-related dispersal may overcome the excess of one sex among fledglings. Thus, a sound explanation of the sex-differential dispersal could be that first-year males outnumbered first-year females suffering higher competition for mating and therefore were more likely to disperse if they failed at their first breeding attempt as juveniles. This is consistent with the

results of our previous study [9] suggesting that more males dispersed along with the increasing population size and, on the other side, it matches our previous suggestion [64] that the bias towards male dispersants could be mainly sustained by juveniles failing at breeding. However, a number of alternative, non-exclusive explanations exist. For instance, the sex-related cost/benefit ratio of dispersal might also be explained by other differences between sexes like territoriality, size dimorphism or by greater proportions of male immigrants (see [65] for a discussion on this).

Often, new colonies are more productive and faster-growing than old colonies ([20,66–68] but see [69,70]) especially when they are promoting the expansion of the species [71] and even if founded by a small number of individuals (see [66] and references therein). Two related processes can explain this phenomenon: (*i*) on the one hand, although new colonies are likely to be fuelled by dispersing, inexperienced individuals, the breeding success may be very high as a result of inhabiting unexploited, good-quality patches with as yet little competition for food (see [20,66,68]); (*ii*) on the other, new and highly productive colonies may attract local and non-local recruiters [16] dispersing from old, saturated colonies with high competition levels [72]. Therefore, breeding success and recruitment may form a positive feedback loop increasing the population growth rate. Our results support the importance of both mechanisms in the dynamics of the studied glossy ibis population. First, we found high productivity (more than two fledglings per pair) compared with other studies on this species (ca. 0.4 – 1 fledglings/pair in North America and Australia; [31,73–75]). High fecundity rates were found also on a recently settled glossy ibis population in Algeria [37] with about 2.7 nestlings per pair alive at twelve days of age (most mortality occurs within the first ten days; [31]). Secondly, local and non-local recruitment rates contributed to the population increase that was steep until 2003. During that period, new immigrants (on average 58

females/year) strongly influenced the population dynamics similar to what was observed among several seabirds' new colonies [20,66–68]. The effect the immigration had on population increase appears substantial as further confirmed by the fact that almost double the recorded mean breeding success would have been necessary to achieve the observed population growth rate. Consistent with the above mentioned positive feedback loop involving productivity, recruitment and growth rate, the observed early age at recruitment might have been related to the high productivity of the colony as found by Frederiksen & Bregnballe [76] with cormorants (*Phalacrocorax carbo sinensis*). Also, high productivity might be favored by low population density during the first years (reviewed by [77]). In birds, it has been shown that the growth rate of long-lived is mostly affected by adult survival whereas that of highly reproductive species depends more on fecundity [4]. However, we found that the glossy ibis growth rate was mostly affected by productivity (Fig. S2) suggesting that although it is a long-lived species (up to 20 years of age; unpublished data and [29]), glossy ibis may achieve very high reproductive outputs key for its population dynamics. Although this is the first long-term data analysis providing an estimate of the age at first breeding, some previous observations in North-America populations suggested that sexual maturity was at three years of age (see [27]) while most individuals recruited as breeders during the first year in the Doñana populations. For example, two studies in North-America found contradictory evidence about the age at first reproduction of glossy ibises that, for a population at the edge of their distribution area, appeared to be one year [31] whereas for others, in the core of their range area, was three years [78]. This heterogeneity may depend on density-dependence effect according to which when a certain population size threshold is reached, age at first reproduction is the first demographic parameter to change (rising) [2].

While it has been shown that immigration can fuel rapid expansion of new colonies (especially of seabirds, e.g. [67]), little is known about the role a newly-established population may play in source/sink dynamics. Several studies support the idea that populations at the edge of their distribution range tend to facilitate dispersal and therefore range expansion by means of behavioral (e.g. aggressiveness; [79]) or life-history characteristics (e.g. fecundity, dispersal propensity; [71,80]). At Doñana, before the formation of satellite glossy ibis colonies, natal recruiters faced two very different strategies: local recruiting or breeding somewhere far away. However, since 2004 they faced a third option: recruiting at a neighbor colony inside Doñana from which resightings data were not collected due to logistical constraints (see [33]). Thus, while until 2003 all the Doñana population bred at the FAO, since 2004 both the local recruitment and the immigration rate we reported, as well as the observed and predicted growth rate, referred uniquely to the FAO portion of the Doñana population which, overall, was still growing after 2004 [32]. Thus, although (Table S3; [8]) the FAO/Doñana population was a potential source through the first period, it is quite possible that the FAO and Doñana population as a whole served as a source for the expansion of the species also through the second period, as supported by many Doñana-born individuals seen breeding elsewhere in the last few years (Fig. 4).

Glossy ibis is catalogued as of conservation concern and in decline in Europe [81]. The origin of the Doñana colonizers and immigrants is uncertain; accordingly to a few recoveries of marked individuals they could proceed from populations breeding in East Europe (Black Sea) and most likely wintering in Western Africa [27]. However, resightings of Doñana native individuals make clear that the metapopulation range includes the Mediterranean basin, Western- and, even though fewer observations are available, Eastern-Europe. As shown in Santoro et al. [32] and supported from other studies on

colonial birds (e.g. [82]), the creation and protection of suitable patches available for breeding are crucial for their conservation. Particularly, as demonstrated by many breeding sites occupied only sporadically (Fig. 4), the glossy ibis is a species adapted to highly variable and unpredictable habitats with great plasticity to disperse when breeding conditions are adverse. Doñana has allowed this species to rapidly expand towards a number of suitable, well-managed and still unexploited areas in the Western Europe and Mediterranean basin. Thus, there is a need for coordinated management policies at a broad scale allowing for the preservation of suitable patches for the breeding of this and other wading birds. On the other hand, this study shows the value of CR and matrix population modeling for understanding the population processes driving range expansion of bird populations. Broader CR studies at multiple colonies across the range of glossy ibis would allow such analyses at the scale of an entire metapopulation, clarifying the rates of dispersal between populations and the costs and benefits of dispersal. Furthermore, if such studies can be integrated with studies of the fine-scale movements of individuals through tracking devices, further insights will be provided.

In conclusion, our study illustrates that the rate of increase of a newly-established population can be boosted by high immigration more than by intrinsic demographic parameters. At the same time, under favorable conditions, this process can be so fast that such a new population can itself become a source population driving range expansion at a strikingly fast rate.

References

1. Le Galliard JF, Massot M, Clobert J (2012) Dispersal and range dynamics in changing climates: a review. In: Clobert J, Baguette M, Benton TG, Bullock JM, editors. Dispersal Ecology and Evolution. Oxford University Press. pp. 318–336. Available: http://books.google.es/books?hl=es&lr=&id=wC9qnr4dH5AC&oi=fnd&pg=PA317&dq=dispersal+and+range+dynamics+in+changing+climates:+a+review&ots=o1vKbP7qBk&sig=-ECj1erMn_-MCDEgAm-QjgZLnvs. Accessed 12 December 2012.

2. Stearns SC (1992) The evolution of life histories. Oxford University Press Oxford.

3. Benton T, Plaistow S, Coulson T (2006) Complex population dynamics and complex causation: devils, details and demography. Proc R Soc B Biol Sci 273: 1173–1181. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1560275&tool=pmcentrez&rendertype=abstract. Accessed 11 July 2014.

4. Sæther S, Bakke Ø (2000) Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81: 642–653.

5. Van Groenendael J, de Kroon H, Caswell H (1988) Projection matrices in population biology. Trends Ecol Evol 3: 264.

6. Doxa A, Besnard A, Bechet A, Pin C, Lebreton J-D, et al. (2013) Inferring dispersal dynamics from local population demographic modelling: the case of the slender-billed gull in France. Anim Conserv 16: 684–693. Available: http://doi.wiley.com/10.1111/acv.12048. Accessed 8 November 2013.

7. Hanski I (1998) Metapopulation dynamics. Nature 396: 41–49.

8. Peery M, Becker B, Beissinger S (2006) Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird. Ecol Appl 16: 1516–1528. Available: http://www.ncbi.nlm.nih.gov/pubmed/16937815.

9. Santoro S, Green AJ, Figuerola J (2013) Environmental Instability as a Motor for Dispersal: A Case Study from a Growing Population of Glossy Ibis. PLoS One 8: e82983. Available: http://dx.plos.org/10.1371/journal.pone.0082983. Accessed 29 December 2013.

10. Jenouvrier S (2013) Impacts of climate change on avian populations. Glob Chang Biol: 1–22. Available: http://doi.wiley.com/10.1111/gcb.12195. Accessed 16 March 2013.

11. Parmesan C (2006) Ecological and Evolutionary Responses to Recent Climate Change. Annu Rev Ecol Syst 37: 637–669. doi:10.2307/annurev.ecolsys.37.091305.30000024.

12. Gaston K (2009) Geographic range limits: achieving synthesis. Proc R Soc B Biol Sci 276: 1395–1406. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2677218&tool=pmcentrez&rendertype=abstract. Accessed 31 August 2014.

13. Stamps J (1988) Conspecific Attraction and Aggregation in Territorial Species. Am Nat 131: 329–347.

14. Smith AT, Peacock MM (1990) Conspecific Attraction and the Determination of Metapopulation Colonization Rates. Conserv Biol 4: 320–323.

15. Oro D, Pradel R (2000) Determinants of local recruitment in a growing colony of Audouin's gull. J Anim Ecol 69: 119–132.

16. Danchin E, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79: 2415–2428.

17. Brown CR, Brown MB, Danchin E (2000) Breeding habitat selection in cliff□ swallows: the e□ffect of conspecific reproductive success on colony choice. J Anim Ecol 69: 133–142.

18. Hernández-Matías A, Real J, Pradel R, Ravayrol A, Vincent-Martin N, et al. (2010) Determinants of Territorial Recruitment in Bonelli's Eagle (Aquila fasciata) Populations. Auk 127: 173–184.

Available: http://www.jstor.org/stable/10.1525/auk.2009.09143. Accessed 8 March 2012.

19. Henaux V, Bregnballe T, Lebreton JJ-D, Hénaux V (2007) Dispersal and recruitment during population growth in a colonial bird, the great cormorant Phalacrocorax carbo sinensis. J Avian Biol 38: 44–57. doi:10.1111/j.2007.0908-8857.03712.x.

20. Porter J, Coulson J (1987) Long-term Changes in Recruitment to the Breeding Group, and the Quality of Recruits at a Kittiwake Rissa tridactyla colony. J Anim Ecol 56: 675–689.

21. Spear L, Sydeman W, Pyle P (1995) Factors affecting recruitment age and recruitment probability in the Western Gull Larus occidentalis. Ibis (Lond 1859) 137: 352–359.

22. Both C, Visser ME, Verboven N (1999) Density-dependent recruitment rates in great tits: the importance of being heavier. Proc R Soc B Biol Sci 266: 465–469. Available: http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.1999.0660. Accessed 28 May 2014.

23. Forslund P, Pärt T (1995) Age and reproduction in birds - hypotheses and tests. Trends Ecol Evol 10: 374–378.

24. Møller A (2006) Sociality, age at first reproduction and senescence: comparative analyses of birds. J Evol Biol 19: 682–689. doi:10.1111/j.1420-9101.2005.01065.x.

25. Krüger O (2005) Age at first breeding and fitness in goshawk Accipiter gentilis. J Anim Ecol 74: 266–273. doi:10.1111/j.1365-2656.2004.00920.x.

26. Newton I (2003) The speciation and biogeography of birds. London: Academic Press. Available: http://www.lavoisier.fr/livre/notice.asp?id=OR3WARAL2LAOWF. Accessed 27 August 2012.

27. Figuerola J, Mañez M, Ibáñez F, García L, Garrido H (2004) Morito común Plegadis falcinellus. Libro rojo de las Aves de España. Dirección general para la Biodiversidad. Madrid: SEO/BirdLife. pp.

74–76. Available: http://www.xoriguer.org/ftpdescarregues/libro_rojo_aves_espana.pdf#page=74. Accessed 22 August 2012.

28. Del Hoyo J, Elliott A, Sargatal J, Cabot J, Jutglar F (1992) Handbook of the birds of the world: IBIS and SPOONBILLS.

29. Davis Jr WE, Kricher J (2000) Glossy Ibis (Plegadis falcinellus). Birds North Am: 20.

30. Hancock JA, Kushlan JA, Kahl MP (1992) Storks, ibises and spoonbills of the world. San Diego, California: Academic Press Ltd.

31. Miller L, Burger J (1978) Factors affecting nesting success of the glossy ibis. Auk 95: 353–361.

32. Santoro S, Mañez M, Green AJ, Figuerola J (2010) Formation and growth of a heronry in a managed wetland in Doñana, southwest Spain. Bird Study 57: 515–524. Available: http://www.tandfonline.com/doi/abs/10.1080/00063657.2010.501371#.UzU_T8fGyqR.

33. Mañez M, Rendón-Martos M (2009) El morito común , la espátula común y el flamenco común en España . Población en 2007 y método de censo. Máñez M, Rendón-Martos M, editors Madrid: SEO/Birdlife.

34. Rendón MA, Green AJ, Aguilera E, Almaraz P (2008) Status, distribution and long-term changes in the waterbird community wintering in Doñana, south–west Spain. Biol Conserv 141: 1371–1388.

35. Kayser Y, Blanchon T, Gauthier-Clerc M, Petit J (2009) L ' Ibis falcinelle Plegadis falcinellus nicheur régulier en Camargue. Ornithos 16: 404–406.

36. Belhadi G, Chalabi B, Chabi Y, Kayser Y, Gauthier-Clerc M (2007) Le retour de l' Ibis falcinelle (Plegadis falcinellus) nicheur en Algérie. Aves 44: 29–36.

37. Boucheker A, Nedjah R, Samraoui F, Menaï R, Samraoui B (2009) Aspects of the Breeding Ecology and Conservation of the

Glossy Ibis in Algeria. Waterbirds 32: 345–351. Available: http://www.bioone.org/doi/abs/10.1675/063.032.0215. Accessed 9 December 2012.

38. Rousseau E (1994) Nouveau cas de reproduction de l'ibis falcinelle Plegadis falcinellus au Maroc. Alauda. Available: http://cat.inist.fr/?aModele=afficheN&cpsidt=3390644. Accessed 9 December 2012.

39. Noivo C, Jara J (2007) First records of breeding Glossy Ibis Plegadis falcinellus in Portugal. Anu Ornitol 5: 133–135.

40. Brichetti P (1986) Nidificazione di Nitticora Nycticorax nutycorax e Mignattaio Plegadis falcinellus in Puglia. Avocetta 10: 59–60.

41. Grussu M (2004) Nuovo sito di nidificazione di Mignattaio, Plegadis falcinellus, in Sardegna. Riv ital Orn 73: 171–173.

42. Marion L, Marion P (2011) Première reproduction prouvée de l'Ibis falcinelle Plegadis falcinellus au lac de Grand-Lieu (Loire-Atlantique). Alauda 79: 215–219. Available: http://cat.inist.fr/?aModele=afficheN&cpsidt=24515795. Accessed 9 December 2012.

43. Griffiths R, Double MC, Orr K, Dawson RJG (1998) A DNA test to sex most birds. Mol Biol 7: 1071–1075.

44. Figuerola J, García L, Green AJ, Ibáñez F, Mañez M, et al. (2006) Sex determination in glossy ibis chicks based on morphological characters. Ardeola 53: 229–235.

45. Caswell H (2001) Matrix population models. John Wiley & Sons, Ltd.

46. Pradel R (2005) Multievent: an extension of multistate capture-recapture models to uncertain states. Biometrics 61: 442–447. doi:10.1111/j.1541-0420.2005.00318.x.

47. Rouan L, Pradel R, Choquet R (2009) Program E-SURGE: A Software Application for Fitting Multievent Models. In: Thomson DL, Cooch EG, Conroy MJ, editors. Series: Environmental and Ecological Statistics. Boston, MA: Springer US. pp. 845–865. Available:

http://www.springerlink.com/index/10.1007/978-0-387-78151-8. Accessed 29 February 2012.

48. Choquet R, Reboulet A-M, Lebreton J-D, Gimenez O, Pradel R (2005) U-CARE 2.2 User's Manual. CEFE, Montpellier, France.

49. Grosbois V, Tavecchia G (2003) Modeling dispersal with capture – recapture data : disentangling decisions of leaving and settlement. Ecology 84: 1225–1236.

50. Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York: Springer-Verlag.

51. Skalski JR, Hoffmann A, Smith SG (1993) Testing the significance of individual-and cohort-level covariates in animal survival studies. In: Lebreton JD, North PM, editors. Marked Individuals in the Study of Bird Population. pp. 9–28. Available: http://scholar.google.es/scholar?q=Testing+the+significance+of+individual+and+covariates+in+animal+survival&hl=es&as_sdt=0&as_ylo=1990&as_yhi=#0. Accessed 23 November 2012.

52. Gimenez O, Choquet R, Lamor L, Scofield P, Fletcher DJ, et al. (2005) Efficient profile-likelihood confidence intervals for capture-recapture models. J Agric Biol Environ Stat 10: 184–196. doi:10.1198/108571105X46462.

53. Tavecchia G, Viedma C, Martínez-Abraín A, Bartolomé MA, Gómez JA, et al. (2009) Maximizing re-introduction success: Assessing the immediate cost of release in a threatened waterfowl. Biol Conserv 142: 3005–3012. Available: http://linkinghub.elsevier.com/retrieve/pii/S0006320709003607. Accessed 24 March 2014.

54. Morris KW, Doak DF (2002) Quantitative conservation biology: the theory and practice of population viability analysis. Sunderland, MA: Sinauer.

55. Stubben C, Milligan B (2007) Estimating and Analyzing Demographic Models Using the popbio Package in R. J Stat Softw 22.

56. Fujiwara M, Caswell H (2002) Estimating population projection matrices from multi-stage mark–recapture data. Ecology 83: 3257–3265.

57. Sarrazin F, Legendre S (2000) Demographic Approach to Releasing Adults versus Young in Reintroductions. Conserv Biol 14: 488–500. Available: http://doi.wiley.com/10.1046/j.1523-1739.2000.97305.x.

58. Carnell R (2012) lhs: Latin hypercube samples.

59. Pujol G, Iooss B, Janon A, Gilquin L, Le Gratiet L, et al. (2014) sensitivity: Sensitivity Analysis.

60. Valone T (1989) Group foraging, public information, and patch estimation. Oikos: 357–363.

61. Boulinier T, Danchin E (1997) The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. Evol Ecol 11: 505–517.

62. Ramo C, Aguilera E, Figuerola J, Mañez M, Green AJ (2013) Long-term population trends of colonial wading birds breeding in Doñana (SW Spain) in relation to environmental and anthropogenic factors. Ardeola 60: 305–326. doi:10.13157/arla.60.2.2013.305.

63. Schaub M, Gimenez O, Schmidt BR, Pradel R (2004) Estimating survival and temporary emigration in the multistate capture-recapture framework. Ecology 85: 2107–2113.

64. Santoro S, Green A (n.d.) Facultative and non-facultative sex ratio adjustments in a dimorphic bird species. Speak J Figuerola, J. doi:10.1111/oik.01889.

65. Clobert J, Baguette M, Benton TG, Bullock JM (2012) Dispersal ecology and evolution. Clobert J, Baguette M, Benton TG, Bullock JM, editors Oxford University Press. Available: http://books.google.es/books?hl=es&lr=&id=wC9qnr4dH5AC&oi=fnd&pg=PP2&dq=dispersal+ecology+and+evolution&ots=o1vK8R4pFh&sig=_8o4y6mC1wpji-_Lsz4m5G_O1Lg. Accessed 9 December 2012.

66. Oro D, Ruxton GD (2001) The formation and growth of seabird colonies: Audouin's gull as a case study. J Anim Ecol 70: 527–535.

67. Kildaw S, Irons D, Nysewander D, Buck C (2005) Formation and growth of new seabird colonies: the significance of habitat quality. Mar Ornithol 58: 49–58.

68. Tims J, Nisbet I, Friar M, Mostello C, Hatch J (2004) Characteristics and Performance of Common Terns in Old and Newly-established Colonies. Waterbirds 27: 321–332.

69. Coulson J, Coulson B (2008) Measuring immigration and philopatry in seabirds; recruitment to Black-legged Kittiwake colonies. Ibis (Lond 1859) 150: 288–299.

70. Martínez-Abraín A, Oro D, Jimenez J (2001) The dynamics of a colonization event in the european shag: the roled of immigration and demographic stochasticity. Waterbirds 24: 97–102.

71. Phillips B (2009) The evolution of growth rates on an expanding range edge. Biol Lett 5: 802–804.

72. Den Boer P (1968) Spreading of risk and stabilization of animal numbers. Acta Biotheor 18: 165–194.

73. Lowe KW (1983) Egg size, clutch size and breeding success of the Glossy Ibis Plegadis falcinellus. Emu 83: 31–34.

74. Burger J (1978) Competition between cattle egrets and native North American herons, egrets, and ibises. Condor 80: 15–23.

75. Williams B (1975) Growth rate and nesting aspects for the Glossy Ibis in Virginia. Raven 46: 35–51.

76. Frederiksen M, Bregnballe T (2001) Conspecific reproductive success affects age of recruitment in a great cormorant, Phalacrocorax carbo sinensis, colony. Proc R Soc B Biol Sci 268: 1519–1526. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1088772&tool=pmcentrez&rendertype=abstract. Accessed 10 September 2014.

77. Balbontín J, Ferrer M (2008) Density-dependence by habitat heterogeneity : individual quality versus territory quality. OIKOS 117: 1111–1114. doi:10.1111/j.2008.0030-1299.16232.x.

78. Byrd M (1978) Dispersal and movements of six North American ciconiiforms. Wading Birds (A. Sprunt IV, JC Ogden and S. Winckler, Eds.). New York, National Audubon Society, Research Report. pp. 161–185.

79. Duckworth RA, Badyaev A V (2007) Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proc Natl Acad Sci U S A 104: 15017–15022. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1986605&tool=pmcentrez&rendertype=abstract.

80. Lindström T, Brown G, Sisson S, Phillips B, Shine R (2013) Rapid shifts in dispersal behavior on an expanding range edge. Proc Natl Acad Sci U S A 110: 13452–13456. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3746873&tool=pmcentrez&rendertype=abstract.

81. Burfield I, van Bommell F (2004) Birds in Europe: Population Estimates, Trends, and Conservation Status. Cambridge (UK): BirdLife International.

82. Perennou C, Sadoul N, Pineau O, Johnson A, Hafner H (1996) Management of nest sites for colonial waterbirds. Conserv Mediterr Wetl No4 Tour du Valat, Arles Fr.

Tables

Table 1. Local recruitment capture-recapture hypotheses testing.

Model no.	Model effects	*np*	Dev	AIC_c	ΔAIC_c	*wi*	*F*1,7	*P*-value	R^2
R1	*cohort (1996-2002 vs. others)*	37	17700.58	17774.96	0.00	0.48	6.39	0.04	0.92
R2	*time (1996-2002 vs. others)*	37	17702.18	17776.56	1.60	0.21	6.27	0.04	0.90
R3	*time*	42	17692.29	17776.79	1.83	0.19			
R4	*cohorts*	42	17693.22	17777.72	2.76	0.12			
R5	*flood- i*	35	17743.67	17814.02	39.05	0.00	3.21	0.12	0.46
R6	*flood- i +1*	35	17747.05	17817.40	42.43	0.00	2.96	0.13	0.43
R7	*time (1996-2002 vs. 2003-2006)*	35	17763.96	17834.30	59.34	0.00	1.72	0.23	0.25
R8	*cohort (1996-2002 vs. 2003-2006)*	35	17765.02	17835.37	60.40	0.00	1.64	0.24	0.24
R9	*population size*	35	17766.54	17836.88	61.92	0.00	1.53	0.26	0.22
R10	*dry years*	35	17783.53	17853.87	78.91	0.00	0.28	0.61	0.04
R11	*constant*	34	17787.28	17855.61	80.65	0.00			
R12	*fecundity*	35	17787.14	17857.49	82.53	0.00	0.01	0.92	0.00

Model notation: *np*, number of estimable parameters; *Dev*, relative deviance; AIC_c, Akaike information criterion corrected for small sample size; ΔAIC_c, the AIC_c difference of the current model with respect to the lowest AIC_c value; w_i, Akaike's weight, *F*1,7, F-statistic; R^2, current model percentage of deviance explained.

Supporting Information

Appendix 1

Multievent probabilistic approach

Multievent models link the information mediated by events to the underlying states to allow the estimate of several parameters without data censoring of encounters with no information on individual's state. As an example, some morphological features may be observed in individuals that might be informative on their sex (male or female): the interpretation given of that feature on the real sex (e.g. visual assessment of sex) would therefore represent the event whereas the sex would represent the underlying state. Three kinds of parameter are common to every multievent model: the Initial State (the probability a first captured individual is in a certain state), the State Transition and the Event (that links the detection probability of events to the detection probability of the underlying states).

Five underlying biological states:
† - Death or permanently emigrated
♀NB - Female non-breeder alive at FAO
♀B - Female breeder alive at FAO
♂NB - Male non-breeder alive at FAO
♂B - Male breeder alive at FAO

Four events, numbered as they appear in the encounter history:
0 - Bird not resighted
1 - Bird resighted, visually identified as a female when it was a chick
2 - Bird resighted, visually identified as a male when it was a chick
3 - Bird resighted, visually unsexed when it was a chick

INITIAL STATE

Here this parameter refers to the probability a first captured individual is a female non-breeder. As all the individuals stated their encounter history when they were marked as chicks, we considered that both a breeder and a dead individual could not be captured at the first encounter. Therefore, the initial state probabilities are:

♀NB	♀B	♂NB	♂B
π	-	1- π	-

π is the probability that a first resighted individual is a non-breeder female.

STATE TRANSITION

We considered two steps for this parameter. Probabilities are here represented in the form of stochastic matrices with departure states in rows and arrival states in columns. Neither transitions between genders nor those between the breeder status to non-breeder's were allowed.

Step 1 – Apparent Survival; this refers to the probability an individual in a certain state in occasion *t* will survive and remain in the area between t and *t* + 1.

	♀NB	♀B	♂NB	♂B	†
♀NB	φ_{fNB}	0	0	0	1- φ_{fNB}
♀B	0	φ_{Fb}	0	0	1- φ_{fB}
♂NB	0	0	φ_{mNB}	0	1- φ_{mNB}
♂B	0	0	1	φ_{mB}	1- φ_{mB}
†	0	0	0	0	1

Where the subscripts *f*, *m*, *NB* and *B* refer respectively to: female, male, non-breeder and breeder.

Step 2 - Recruitment (conditional on Apparent Survival); this refers to the probability an individual still alive and in the area in *t* + 1, has of recruiting at the colony (an individual seen at the colony is assumed to be a breeder) between *t* and *t* + 1 (ψ).

	♀NB	♀B	♂NB	♂B	†
♀NB	1- ψ_f	ψ_f	0	0	0
♀B	0	1	0	0	0
♂NB	0	0	1- ψ_m	ψ_m	0
♂B	0	0	0	1	0
†	0	0	0	0	1

Same notation as above for the subscripts.

EVENT

The Event probabilities couple the events to the underlying biological states. We have considered three steps.

Step 1 - Resighting; This estimates the probability (β) one individual has to be resighted at *t* + 1.

	not seen	live ♀ seen	live ♂B seen
♀NB	1 - β_f	β_f	0
♀B	1 – β_f	β_f	0
♂NB	1 – β_m	0	β_m
♂B	1 – β_m	0	β_m
†	1	0	0

Same notation as above for the subscripts.

Step 2 - Visual Sexing (conditional on Resighting); this estimates, conditional on being resighted, the probability (γ) one individual has to be visually sexed when it was a chick.

	not seen	not sexed	live ♀ sexed	live ♂sexed
not seen	1	0	0	0
live ♀ seen	0	1 - γ_f	γ_f	0
live ♂ seen	0	1 – γ_m	0	1 – γ_m

Same notation as above for the subscripts.

Step 3 - Correctness (conditional on Resighting and Visual Sexing); This estimates, conditional on being resighted and visually sexed, the probability (δ) an individual has of being correctly visually sexed as a female or a male.

	0	1	2	3
not seen	1	0	0	0
not sexed	0	0	0	1
live ♀ sexed	0	δ_f	$1 - \delta_f$	0
live ♂sexed	0	$1 - \delta_m$	δ_m	0

Same notation as above for the subcripts

Model Selection approach

Model selection was based on four criteria. As a general rule, throughout the model simplification process we retained the model whose AIC_c was at least 2 units lower; in case the models AIC_c difference was smaller than 2 units, the least parameterized model was retained [1]. In the first step, we modeled Resighting and Initial State; we kept both Visual Sexing and Correctness to depend on birth year according to previous analyses [2]. In step two, we used the best model structure so far obtained and modeled both Survival and Recruitment while keeping the more general settings of the other parameter (respectively Recruitment and Survival). To limit the possible effect of the modeling order, in step three, we ran all the possible combinations of best model structures found in Survival and Recruitment modeling (i.e. for each parameter type models within $2\Delta AIC_c$ from the best model). Finally, in step four, we focused on the parameter we considered of primary interest: Recruitment. We used the best model resulting from step three to testing hypotheses.

REFERENCES:

1. Burnham KP, Anderson DR: *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd ed. New York: Springer-Verlag; 2002.
2. Santoro S, Green AJ, Figuerola J: Environmental Instability as a Motor for Dispersal: A Case Study from a Growing Population of Glossy Ibis. *PLoS One* 2013, **8**:e82983.

APPENDIX 2

Growth population rates, immigrants and sensitivity

First, the observed growth population rate was estimated by following procedure suggested in Morris & Doak [1] on counts data obtained at the FAO colony. Secondly, we calculated the predicted growth population rate if it had depended exclusively on the intrinsic demographic parameters (survival, local recruitment and productivity). With this purpose we used a matrix population model parameterized with the 95%CI estimates obtained from capture-recapture analyses (survival and local recruitment) and count sessions (productivity). It should be noted that whereas the observed population size depends on birth, death, immigration and emigration, the matrix-predicted growth depends on birth, death and emigration (that are indistinguishable between them) but not on immigration. Then, if estimates are accurate, the difference, if any, between the observed and matrix-predicted growth rates must be due to immigration. For details on field-work protocol to get count and productivity data at the colony see [2,3]. In a third step we used the same set of simulations to estimate the effect of any intrinsic rate on the predicted growth rate (sensitivity analysis). Finally, in a fourth step, in case the observed growth rate significantly exceeded the matrix-predicted, we used a deterministic approach consisting of a matrix population model that included an immigration class (see [4,5]), then the number of female immigrants needed to achieve the observed population size was computed by an iterative process (n= 10,000). The credible confidence interval was estimated by calculating the 0.025 and 0.975 distribution quantiles.
Below are reported the R scripts with commentaries used for these analyses.

```
library(sensitivity)
library(lhs)
library(popbio)

# ------------------------------------------------------------------
# -------------------------STEP 1 - OBSERVED LAMBDA-------------------
--
#       ------------------------------------------------------------------#
Calculating the observed growth rate by using the regression
procedure detailed
# in Morris & Doak (2002 - Ch.3)
pop.size<-as.numeric(c(7,40,84,73,199,400,668,705,700,1500))    #
Population size
year<-(c(1996,1997,1998,2000,2001,2002,2003,2004,2006,2007))
```

```
bs<-
as.numeric(c(2.429,1.9,1.405,2.301,2.075,2.5,2.246,3.511,2.097,3.
134)) # Breeding success
popdata<-data.frame(pop.size,year,bs) # Creating the data set

 # First period (1996-2003):
popdata9603<-popdata[1:7,]
y1<-numeric(0)
x1<-numeric(0)
for (i in 1:6){
      y1[i]<-
log((popdata9603$pop.size[i+1]/popdata9603$pop.size[i]))/(sqrt((po
pdata9603$year[i+1]-popdata9603$year[i])))
      x1[i]<-sqrt((popdata9603$year[i+1]-popdata9603$year[i]))
}
# Calculating the regression coefficient and residual mean square
which I need to calculate the lambda and the SE:
reg9603<-lm(y1~x1+0) # Running the regression
coef(reg9603) # coefficient of regression
lobs1<-exp(coef(reg9603)) # Observed lambda for the first period
(1996 - 2003)

# CI of lambda observed for the first period
round(exp((coef(reg9603)-
1.96*SElobs1)),3);round(exp((coef(reg9603)+1.96*SElobs1)),3)


# Second period (2004-2007):
popdata0307<-popdata[7:10,]
y2<-numeric(0)
x2<-numeric(0)
for (i in 1:3){
      y2[i]<-
log((popdata0307$pop.size[i+1]/popdata0307$pop.size[i]))/(sqrt((po
pdata0307$year[i+1]-popdata0307$year[i])))
      x2[i]<-sqrt((popdata0307$year[i+1]-popdata0307$year[i]))
}
reg0307<-lm(y2~x2+0)
coef(reg0307)
lobs2<-exp(coef(reg0307))
SElobs2<-sqrt(mean(reg0307$residuals^2)/3)
round(exp((coef(reg0307)-
1.96*SElobs2)),3);round(exp((coef(reg0307)+1.96*SElobs2)),3)
```

```
# ------------------------------------------------------------------
# ---------STEP 2 & 3 - PREDICTED LAMBDA AND SENSITIVITY ANALYSIS-----
# ------------------------------------------------------------------
# Analogously, to calculate the 95%CI of the breeding success:
# first period:
meanbs1<-mean(popdata9603$bs) # mean breeding success period
SEmeanbs1<-sd(popdata9603$bs) # Standard Error
#second period:
meanbs2<-mean(popdata0407$bs)
SEmeanbs2<-sd(popdata0407$bs)

# ------------------------------------------------------------------
# ----------------------Lambda First Period-------------------------
# ------------------------------------------------------------------
# Since the survival estimate of adult female non-breeders was at the boundary and the 95%CI was calculated by using the profile likelihood (see Methods section in the manuscript), the standard error was calculated at posteriori from the lower confidence interval as:
femSE<-(0.999-0.782)/1.96

# I create two data frames containing random combinations of the estimated demographic parameters (female only) according to a normal distribution and the estimated error estimate. By doing so I can create a matrix that will be used to bootstrap the Leslie model matrix in order to get an error estimate of the predicted lambda
set.seed(10012023)
p1<-randomLHS(10000, 6)
p1[,1]<-qnorm(p1[,1], mean=0.73648558, sd=0.0293175) # CR survival estimate for 1st year individual
p1[,1]<-ifelse(p1[,1]>1,1,p1[,1]) # A probability cannot be > 1
p1[,2]<-qnorm(p1[,2], mean=0.999, sd=femSE) # CR survival estimate of adult non-breeder
p1[,2]<-ifelse(p1[,2]>1,1,p1[,2])
p1[,3]<-qnorm(p1[,3], mean=0.76367997, sd=0.02568086) # CR survival estimate of adult breeder
p1[,3]<-ifelse(p1[,3]>1,1,p1[,3])
p1[,4]<-qnorm(p1[,4], mean=0.75743072, sd=0.00446794) # CR 1st year recruitment estimate
p1[,4]<-ifelse(p1[,4]>1,1,p1[,4])
p1[,5]<-qnorm(p1[,5], mean=0.37289855, sd=0.09853772) # CR adult recruitment estimate
p1[,5]<-ifelse(p1[,5]<0,0,p1[,5])
```

```
p1[,6]<-qnorm(p1[,6], mean=meanbs1, sd=SEmeanbs1) # count-derived mean breeding succes
p1<-as.data.frame(p1)
colnames(p1)<-c("phi1","phi2nb","phi2b","psi1","psi2","f")

p2<-randomLHS(10000, 6)
p2[,1]<-qnorm(p2[,1], mean=0.73648558, sd=0.0293175) # CR survival estimate for 1st year individual
p2[,1]<-ifelse(p2[,1]>1,1,p2[,1]) # A probability cannot be > 1
p2[,2]<-qnorm(p2[,2], mean=0.999, sd=femSE) # CR survival estimate of adult non-breeder
p2[,2]<-ifelse(p2[,2]>1,1,p2[,2])
p2[,3]<-qnorm(p2[,3], mean=0.76367997, sd=0.02568086) # CR survival estimate of adult breeder
p2[,3]<-ifelse(p2[,3]>1,1,p2[,3])
p2[,4]<-qnorm(p2[,4], mean=0.75743072, sd=0.00446794) # CR 1st year recruitment estimate
p2[,4]<-ifelse(p2[,4]>1,1,p2[,4])
p2[,5]<-qnorm(p2[,5], mean=0.37289855, sd=0.09853772) # CR adult recruitment estimate
p2[,5]<-ifelse(p2[,5]<0,0,p2[,5])
p2[,6]<-qnorm(p2[,6], mean=meanbs1, sd=SEmeanbs1) # count-derived mean breeding succes
p2<-as.data.frame(p2)
colnames(p2)<-c("phi1","phi2nb","phi2b","psi1","psi2","f")


# Parameters dataframe
sa<-sobol2002(model=NULL,p1,p2,nboot=10000,conf=0.95)
pars<-sa$X
# Preparing the loop for calculating predicted lambda (dominant eigenvector of the Leslie matrix):
lambda.pred1<-numeric(0)
phi1<-numeric(0)
phi2nb<-numeric(0)
phi2b<-numeric(0)
psi1<-numeric(0)
psi2<-numeric(0)
f<-numeric(0)
f1<-numeric(0)
f2<-numeric(0)
f3<-numeric(0)
f4<-numeric(0)
f5<-numeric(0)
k1<-numeric(0)
k2<-numeric(0)
k3<-numeric(0)
```

```
m1<-numeric(0)
m2<-numeric(0)
m3<-numeric(0)

for(i in 1:80000){
       sigma=0.5
       phi1[i]<-pars[i,1]
       phi2nb[i]<-pars[i,2]
       phi2b[i]<-pars[i,3]
       psi1[i]<-pars[i,4]
       psi2[i]<-pars[i,5]
       f[i]<-pars[i,6]

       f1[i]= sigma*f[i]*phi1[i]*psi1[i]
       f2[i] = sigma*f[i]*phi2nb[i]*psi2[i]
       f3[i] = sigma*f[i]*phi2nb[i]*psi2[i]
       f4[i] = sigma*f[i]*phi2b[i]*1
       f5[i] = sigma*f[i]*phi2b[i]*1

       k1[i] = phi1[i]*(1-psi1[i])
       k2[i]= phi2nb[i]*(1-psi2[i])
       k3[i]= phi2nb[i]*(1-psi2[i])

       m1[i]= phi1[i]*psi1[i]
       m2[i] = phi2nb[i]*psi2[i]
       m3[i] = phi2nb[i]*psi2[i]

   #--- Leslie matrix ----#
   stages<-c("CH", "NB-J", "NB-A", "B-J", "B-A")
   B<-matrix(c(
   f1[i], f2[i], f3[i], f4[i], f5[i],
   k1[i],  0,  0,  0,  0,
   0,  k2[i],  k3[i],  0,  0,
   m1[i],  0,  0,  0,  0,
   0,  m2[i],  m3[i],  phi2b[i], phi2b[i]
   ), ncol=5, byrow=TRUE,
   dimnames=list(stages,stages)
   )
      lambda.pred1[i]<-(eigen.analysis(B))$lambda1
}
# sensitivity indices
tell(sa,y=lambda.pred1)
# getting the 95%CI estimate of the predicted lambda
mean(lambda.pred1)+(1.96*sd(lambda.pred1))
mean(lambda.pred1)-(1.96*sd(lambda.pred1))
mean(lambda.pred1)
sd(lambda.pred1)
```

```
# ------------------------------------------------------------------
# ----------------------Lambda Second Period 2003-2007--------------
-
# ------------------------------------------------------------------
set.seed(10012023)
p1<-randomLHS(10000, 6)
p1[,1]<-qnorm(p1[,1], mean=0.73648558, sd=0.0293175) # CR
survival estimate for 1st year individual
p1[,1]<-ifelse(p1[,1]>1,1,p1[,1]) # A probability cannot be > 1
p1[,2]<-qnorm(p1[,2], mean=0.999, sd=femSE) # CR survival
estimate of adult non-breeder
p1[,2]<-ifelse(p1[,2]>1,1,p1[,2])
p1[,3]<-qnorm(p1[,3], mean=0.76367997, sd=0.02568086) # CR
survival estimate of adult breeder
p1[,3]<-ifelse(p1[,3]>1,1,p1[,3])
p1[,4]<-qnorm(p1[,4], mean=0.4790024, sd=0.04932053) # CR 1st
year recruitment estimate
p1[,4]<-ifelse(p1[,4]>1,1,p1[,4])
p1[,5]<-qnorm(p1[,5], mean=0.14899738, sd=0.04780904) # CR
adult recruitment estimate
p1[,5]<-ifelse(p1[,5]<0,0,p1[,5])
p1[,6]<-qnorm(p1[,6], mean=meanbs1, sd=SEmeanbs1) # using
the estimate from period I (see Methods in manuscript)
p1<-as.data.frame(p1)
colnames(p1)<-c("phi1","phi2nb","phi2b","psi1","psi2","f")

p2<-randomLHS(10000, 6)
p2[,1]<-qnorm(p2[,1], mean=0.73648558, sd=0.0293175) # CR
survival estimate for 1st year individual
p2[,1]<-ifelse(p2[,1]>1,1,p2[,1]) # A probability cannot be > 1
p2[,2]<-qnorm(p2[,2], mean=0.999, sd=femSE) # CR survival
estimate of adult non-breeder
p2[,2]<-ifelse(p2[,2]>1,1,p2[,2])
p2[,3]<-qnorm(p2[,3], mean=0.76367997, sd=0.02568086) # CR
survival estimate of adult breeder
p2[,3]<-ifelse(p2[,3]>1,1,p2[,3])
p2[,4]<-qnorm(p2[,4], mean=0.4790024, sd=0.04932053) # CR 1st
year recruitment estimate
p2[,4]<-ifelse(p2[,4]>1,1,p2[,4])
p2[,5]<-qnorm(p2[,5], mean=0.14899738, sd=0.04780904) # CR
adult recruitment estimate
p2[,5]<-ifelse(p2[,5]<0,0,p2[,5])
p2[,6]<-qnorm(p2[,6], mean=meanbs1, sd=SEmeanbs1) # count-
derived mean breeding success from period I
p2<-as.data.frame(p2)
colnames(p2)<-c("phi1","phi2nb","phi2b","psi1","psi2","f")
```

```
# Parameters dataframe
sa3<-sobol2002(model=NULL,p1,p2,nboot=10000,conf=0.95)
pars3<-sa3$X
# Calculate model output
lambda.pred3<-numeric(0)
phi1<-numeric(0)
phi2nb<-numeric(0)
phi2b<-numeric(0)
psi1<-numeric(0)
psi2<-numeric(0)
f<-numeric(0)
f1<-numeric(0)
f2<-numeric(0)
f3<-numeric(0)
f4<-numeric(0)
f5<-numeric(0)
k1<-numeric(0)
k2<-numeric(0)
k3<-numeric(0)
m1<-numeric(0)
m2<-numeric(0)
m3<-numeric(0)

for(i in 1:80000){
        sigma=0.5
        phi1[i]<-pars3[i,1]
        phi2nb[i]<-pars3[i,2]
        phi2b[i]<-pars3[i,3]
        psi1[i]<-pars3[i,4]
        psi2[i]<-pars3[i,5]
        f[i]<-pars3[i,6]

        f1[i]= sigma*f[i]*phi1[i]*psi1[i]
        f2[i] = sigma*f[i]*phi2nb[i]*psi2[i]
        f3[i] = sigma*f[i]*phi2nb[i]*psi2[i]
        f4[i] = sigma*f[i]*phi2b[i]*1
        f5[i] = sigma*f[i]*phi2b[i]*1

        k1[i] = phi1[i]*(1-psi1[i])
        k2[i]= phi2nb[i]*(1-psi2[i])
        k3[i]= phi2nb[i]*(1-psi2[i])

        m1[i]= phi1[i]*psi1[i]
        m2[i] = phi2nb[i]*psi2[i]
        m3[i] = phi2nb[i]*psi2[i]

    #--- Leslie matrix ----#
    stages<-c("CH", "NB-J", "NB-A", "B-J", "B-A")
```

```
    B<-matrix(c(
    f1[i], f2[i], f3[i], f4[i], f5[i],
    k1[i],  0,  0,  0,  0,
    0,  k2[i],  k3[i],  0,  0,
    m1[i],  0,  0,  0,  0,
    0,  m2[i],  m3[i],  phi2b[i], phi2b[i]
    ), ncol=5, byrow=TRUE,
    dimnames=list(stages,stages)
    )
       lambda.pred3[i]<-(eigen.analysis(B))$lambda1
}
# sensitivity indices
tell(sa3,y=lambda.pred3)
# getting the 95%CI estimate of the predicted lambda
mean(lambda.pred3) #1.264821 = 1.286177
mean(lambda.pred3)+(1.96*sd(lambda.pred3))
mean(lambda.pred3)-(1.96*sd(lambda.pred3))
mean(lambda.pred3) #1.265 (1.103 - 1.426)
sd(lambda.pred3) #0.082
```

Sensitivity graphics for both periods were extrapolated by sensitivity indices ('sa1' and 'sa3').

```
# ----------------------------------------------------------------
# ------------------ STEP 4 - IMMIGRANTS (only first period) --------
# ----------------------------------------------------------------
phi1<-numeric(0)
phi2nb<-numeric(0)
phi2b<-numeric(0)
psi1<-numeric(0)
psi2<-numeric(0)
f<-numeric(0)
f1<-numeric(0)
f2<-numeric(0)
f3<-numeric(0)
f4<-numeric(0)
f5<-numeric(0)
k1<-numeric(0)
k2<-numeric(0)
k3<-numeric(0)
m1<-numeric(0)
m2<-numeric(0)
m3<-numeric(0)
sigma=0.5 # sex ratio
```

```
duration<-7 # 1996 - 2003
n0<-c(1,0,0,0,0,7) # Initial number of female breeders in 1996
immig1<-numeric(0) # vector to gather the estimated number of immigrants needed to achieve the observed population size under different scenarios according to the 95%CI estimates of demographic parameters
w1<-numeric(0)
popT1<-numeric(0) # vector to gather the number of breeding females predicted by iteratively testing each number of immigrants
popObs1a<-popdata9603$pop.size[7]# 668 number of breeding pairs at the end of the first period
for (i in 1:80000){
	phi1[i]<-pars[i,1]
	phi2nb[i]<-pars[i,2]
	phi2b[i]<-pars[i,3]
	psi1[i]<-pars[i,4]
	psi2[i]<-pars[i,5]
	f[i]<-pars[i,6]


	f1[i]= sigma*f[i]*phi1[i]*psi1[i]
	f2[i] = sigma*f[i]*phi2nb[i]*psi2[i]
	f3[i] = sigma*f[i]*phi2nb[i]*psi2[i]
	f4[i] = sigma*f[i]*phi2b[i]*1
	f5[i] = sigma*f[i]*phi2b[i]*1

	k1[i] = phi1[i]*(1-psi1[i])
	k2[i]= phi2nb[i]*(1-psi2[i])
	k3[i]= phi2nb[i]*(1-psi2[i])

	m1[i]= phi1[i]*psi1[i]
	m2[i] = phi2nb[i]*psi2[i]
	m3[i] = phi2nb[i]*psi2[i]
		for(I in 1:200){
		stages<-c("immig","CH", "NB-J", "NB-A", "B-J", "B-A")
	A<-matrix(c(
	1,0,0,0,0,0,
	f5[i],f1[i], f2[i], f3[i], f4[i], f5[i],
	0,k1[i],  0,  0,  0,  0,
	0,0,  k2[i],  k3[i],  0,  0,
	0,m1[i],  0,  0,  0,  0,
	I,0,  m2[i],  m3[i],  phi2b[i], phi2b[i]
	), ncol=6, byrow=TRUE,
	dimnames=list(stages,stages)
	)
		pop1<-pop.projection(A, n0, duration)		#
projection
```

```
            popT1[I]<-sum(pop1$stage.vectors[3:6,duration])  #
gather the number of breeding females predicted by iteratively
testing each number of immigrants
            }
            w1<-abs(popT1-popObs1a)        # find the number of
immigrants that minimize the difference between the predicted and
observed numbers of female breeders
            immig1[i]<-which(w1==min(w1))
}
# Using median and quartiles to estimate the credible interval for
number of immigrants needed to achieve the observed population
size:
median(immig1)
quantile(immig1,0.025);quantile(immig1,0.975)
```

REFERENCES

1. Morris KW, Doak DF (2002) Quantitative conservation biology: the theory and practice of population viability analysis. Sunderland, MA: Sinauer.
2. Santoro S, Mañez M, Green AJ, Figuerola J (2010) Formation and growth of a heronry in a managed wetland in Doñana, southwest Spain. Bird Study 57: 515–524. Available: http://www.tandfonline.com/doi/abs/10.1080/00063657.2010.501371#.UzU_T8fGyqR.
3. Mañez M, Rendón-Martos M (2009) El morito común , la espátula común y el flamenco común en España . Población en 2007 y método de censo. Máñez M, Rendón-Martos M, editors Madrid: SEO/Birdlife.
4. Sarrazin F, Legendre S (2000) Demographic Approach to Releasing Adults versus Young in Reintroductions. Conserv Biol 14: 488–500. Available: http://doi.wiley.com/10.1046/j.1523-1739.2000.97305.x.
5. Doxa A, Besnard A, Bechet A, Pin C, Lebreton J-D, et al. (2013) Inferring dispersal dynamics from local population demographic modelling: the case of the slender-billed gull in France. Anim Conserv 16: 684–693. Available: http://doi.wiley.com/10.1111/acv.12048. Accessed 8 November 2013.

Table S1. Resighting map. Data from which the map of resightings (Figure 4) has been drawn. Notation: *Lat*, latitude; *Lon*, longitude; *Country*, country; *1st Year*, the year when the first resighting in that location was made; *Breeding*, breeding status of resighted individuals (0= unknown, 1= at least one resighted individual known to be breeding); *N*, total number of resightings in that location.

Lat	Lon	Country	1st Year	Breeding	*N*
30.360	-9.600	Morocco	1999	0	54
43.450	-0.733	France	2005	0	1
43.320	-1.230	France	2005	0	2
49.820	10.420	Germany	2005	0	4
37.090	-8.328	Portugal	2005	0	1
38.280	-8.180	Portugal	2005	0	1
40.440	-8.360	Portugal	2005	0	8
39.230	-8.320	Portugal	2005	0	18
43.517	-5.867	SPain	2005	0	1
42.517	-1.700	Spain	2005	0	1
43.550	-5.600	Spain	2005	0	3
39.067	-3.600	Spain	2005	1	3
43.267	-8.317	Spain	2005	0	10
37.010	9.040	Tunisy	2005	0	2
35.317	25.317	Greece	2006	0	1
45.083	8.667	Italy	2006	1	1
41.013	14.076	Italy	2007	0	1
47.380	20.500	Hungary	2008	0	1
38.441	-8.767	Portugal	2008	0	2
38.077	-8.791	Portugal	2008	0	13
38.200	-0.594	Spain	2008	0	4
36.844	7.987	Algeria	2009	1	1
37.979	23.716	Greece	2009	0	1
38.150	24.033	Greece	2009	0	1
38.440	-8.540	Portugal	2009	0	2
36.783	7.050	Algeria	2010	1	6
36.490	7.540	Algeria	2010	1	7

43.594	4.544	France	2010	1	26
47.683	21.083	Hungary	2010	0	1
47.009	21.806	Romania	2010	0	1
39.225	-0.282	Spain	2011	0	7
42.578	27.610	Bulgaria	2012	0	3
47.374	-2.197	France	2012	0	1
43.648	1.328	France	2012	0	2
45.828	-1.059	France	2012	0	2
43.817	11.167	Italy	2012	0	2
34.282	-6.629	Morocco	2012	1	4
35.783	-5.349	Morocco	2012	0	34
35.120	-6.080	Morocco	2012	0	54
48.679	22.057	Slovakia	2012	0	1
38.617	0.017	Spain	2012	0	1
42.649	-9.038	Spain	2012	0	1
42.988	-7.538	Spain	2012	0	1
43.272	-8.273	Spain	2012	0	1
43.348	-2.659	Spain	2012	0	1
38.928	-6.364	Spain	2012	0	5
43.333	-4.033	Spain	2012	0	5
38.867	-7.013	Spain	2012	1	5
36.226	-5.796	Spain	2012	1	8
43.533	-5.385	Spain	2012	0	11
40.783	0.733	Spain	2012	0	15
51.717	0.467	United Kingdom	2012	0	2
57.166	-2.083	United Kingdom	2012	0	2
36.783	11.983	Italy	2014	0	1
36.733	-4.750	Spain	2014	0	1
47.583	8.243	Switzerland	2014	0	1

Table S2. Model selection. The model selection procedure consisted of five consecutive steps, one for each one of the following parameter types: Resighting (p of being resighted at a given occasion), Initial State (p of being a female when first captured and marked at a given occasion), Survival (p of local survival between *t* and *t* +1), Recruitment (conditioned on Survival, p of recruiting at the colony between *t* and *t* + 1). The other two parameter types, Visual Sexing (p an individual had of being visual sexed at the marking occasion) and Correctness (p that the visual sex matched the real sex), were maintained as depending on cohort as indicated by previous analyses (see [1]). At the end of each step (modeling for a given parameter type, the structure from the best model was retained (the correspondent row is in bold) for the rest of models to be run; in case models with similar AIC_c values (within 2 AIC_c from the lowest AIC_c) existed, the structure from the least parameterized model was held [2]. Parameter types were modeled in the same order (up to down) as they appear in the table but Survival and Recruitment were first modeled by keeping the most parameterized structure of the other. Afterwards, in the last step all the possible combinations between the best models' structure (within 2 AIC_c from the lowest AIC_c) found in Survival and Recruitment (see [1,3] for an analogous procedure) were run. This was done in order to find the best model from which the effect of extrinsic factors on Survival and Recruiment had to be tested (see Table 1) and to avoid bias due to the model selection order. Model notation: *np*, no. of parameters; *Dev*, Deviance; AIC_c, Akaike Information Criterion corrected for small samples; ΔAIC_c, AIC_c difference of the current model with respect to the lowest AIC_c value; *sex*, male or female; *juv*, 1st year individuals; *ad*, adults; *breed*, breeding status; t, temporal variation (years); +, additive effect; *, interactive effect.

	Model's name and effects	*np*	*Dev*	AIC_c	ΔAIC_c
Resighting	RES-3 sex + t	59	17670.75	17789.72	0
	RES-2 t	58	17673.42	17790.37	0.65
	RES-1 sex * t	67	17655.34	17790.60	0.88
Initial State	IS-2 constant	51	17678.88	17781.61	0
	IS-1 t	58	17673.42	17790.37	8.80
Survival	S-2 juv + (ad * sex * breed)	50	17678.90	17779.61	0
	S-1 (juv * sex) + (ad * sex * breed)	51	17678.88	17781.61	2.01
	S-3 juv + (ad * sex)	48	17686.18	17782.83	3.22
	S-4 juv + (ad * breed)	48	17692.22	17788.87	9.26

		S-5 juv + ad	47	17694.72	17789.34	9.73
Recruitment		R-3 age + t	42	17692.70	17777.20	0
		R-2 age + sex + t	43	17692.29	17778.82	1.61
		R-1 age + (sex * t)	51	17678.88	17781.61	4.41
		R-5 t	41	17713.90	17796.37	19.17
		R-4 age + t	42	17713.78	17798.28	21.07
Survival & Recruitment	~t	SR-2 S juv + (ad * sex * breed) R age + sex + t	42	17692.29	17776.79	0
		SR-4 S (juv * breed) + (ad * sex * breed) R age + t	42	17692.70	17777.20	0.41
		SR-4 S (juv * breed) + (ad * sex * breed) R age + sex + t	43	17692.29	17778.82	2.03
		SR-1 S juv + (ad * sex * breed) R age + t	41	17699.86	17782.34	5.54

Table S3. Source – Sink Criteria. How count-derived and projection matrix population growth rates relate affects dynamics of a single population (adapted from [4]). Model notation: λ_C is the rate of population change based upon a times series of population size estimates or indices and λ_M is the rate of population change estimated with a projection matrix model which considers only local recruitment. Then, λ_C may differ from λ_M since the latter does not include immigration processes.

Population Growth rates			Description of Population Dynamics		
λ_C	λ_M	$\lambda_C - \lambda_M$	Population Trend	Immigration → 0	Population Status
< 1	< 1	= 0	declining	no change	declining
< 1	< 1	> 0	declining	faster decline	declining sink
≥ 1	< 1	> 0	stable or increasing	decline	sink
= 1	= 1	= 0	stable	no change	closed or source
> 1	> 1	= 0	increasing	no change	closed or source
> 1	= 1	> 0	increasing	stabilize	open, potential source
> 1	> 1	> 0	increasing	slower increase	open, potential source

REFERENCES

1. Santoro S, Green AJ, Figuerola J (2013) Environmental Instability as a Motor for Dispersal: A Case Study from a Growing Population of Glossy Ibis. PLoS One 8: e82983. Available: http://dx.plos.org/10.1371/journal.pone.0082983. Accessed 29 December 2013.
2. Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York: Springer-Verlag.
3. Grosbois V, Tavecchia G (2003) Modeling dispersal with capture – recapture data : disentangling decisions of leaving and settlement. Ecology 84: 1225–1236.
4. Peery M, Becker B, Beissinger S (2006) Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird. Ecol Appl 16: 1516–1528. Available: http://www.ncbi.nlm.nih.gov/pubmed/16937815.

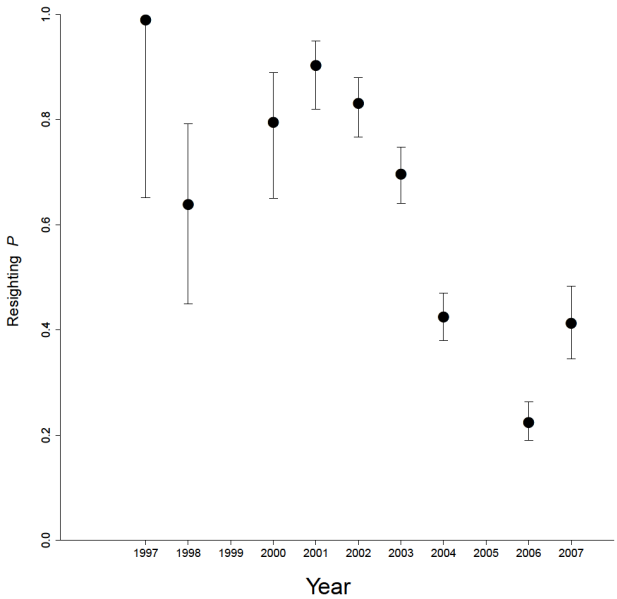

Figure S1. Probability of resighting. Probability of resighting during the breeding season (April – July) at the FAO of glossy ibises born in this colony. Mean and ninety-five % confidence interval estimates are from the most parsimonious model (lowest AICc) found through the entire model selection process.

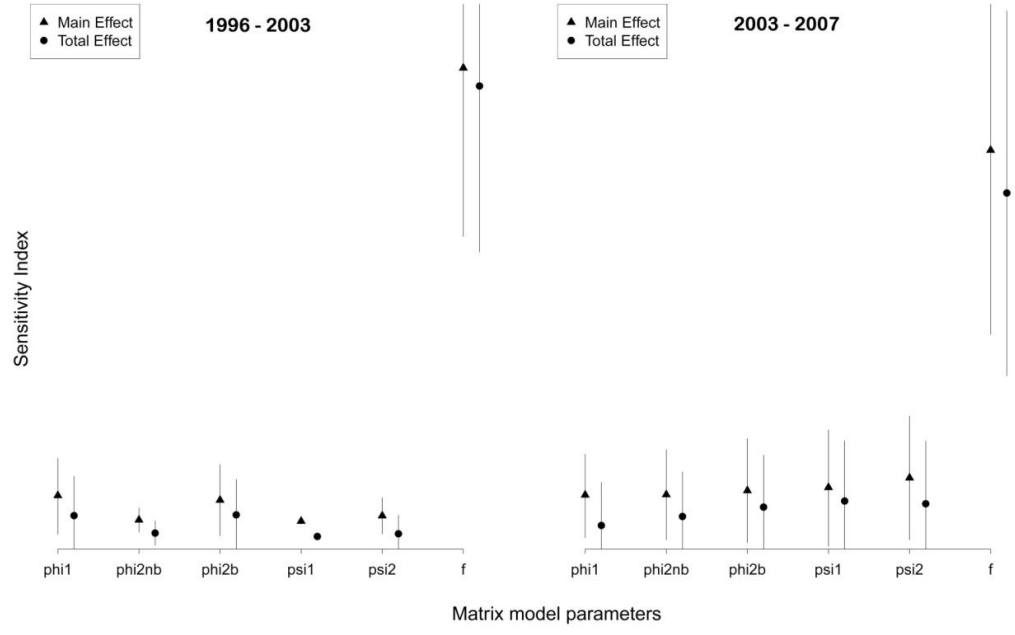

Figure S2. Sensitivity analysis. Mean and ninety-five % confidence interval estimates of first order (circles) and total (triangles) sensitivity Sobol Index values for demographic parameters setting up the projection matrix model used for each period (1996 – 2003; 2003 – 2007). Empty symbols refer to the first period (1996 - 2003) and filled symbols to the second period (2003 - 2007). Notation: *phi1*, local survival of juveniles; *phi2*, local survival of adults; *psi1*, local recruitment of juveniles; *psi*, local recruitment of adults; *f*, fecundity (average number of fledglings per pair).

Capítulo 4

Environmental Instability as a Motor for Dispersal: A Case Study from a Growing Population of Glossy Ibis

Simone Santoro[1], Andy J. Green[1], and Jordi Figuerola[1]
1 Department of Wetland Ecology, Doñana Biological Station-CSIC, Avda. Américo Vespucio s/n, 41092, Seville, Spain

Keywords: Multievent models, Doñana, wetland, uncertainty, E-SURGE, apparent survival

Santoro, S., Green, A. J., & Figuerola, J. (2013). Environmental Instability as a Motor for Dispersal: A Case Study from a Growing Population of Glossy Ibis. PLoS ONE, 8(12), e82983. doi:10.1371/journal.pone.0082983

Summary

Dispersal is a life-history trait directly affecting population dynamics and species range shifts and thus playing a prominent role in the response to climate change. Nonetheless, the relationship between extreme climatic events and dispersal has received little attention in birds. Here we focused on climatic, demographic and individual factors affecting the dispersal propensity of a major glossy ibis population.

We performed a capture-resighting analysis on individuals born and observed at Doñana (South-West Spain) over fourteen years. We applied a multiple analytical approach to show that single-site capture-resighting estimates were a reliable index of dispersal propensity from the area. We focused on the emigration of Doñana-born individuals sporadically (transients) and regularly (residents) frequenting their natal area.

Droughts during two out of 14 study years caused higher apparent dispersal rates, explaining most of the annual variation in these rates. The age structure of Doñana-born individuals resighted simultaneously locally and in Morocco in one week over the 2010 autumn confirmed that the 2005 drought boosted permanent emigration. As numbers increased steadily during non-drought years since the formation of the colony in 1996 to several thousand pairs, philopatry increased gradually, while transients probability appeared to be related to average breeding success. Age, sex, density, quality of foraging habitat and breeding success in the previous season were not found to directly affect apparent dispersal. Nonetheless, autumn sex ratio gradually switched from male (≈ 0.68) to female-skewed (≈ 0.44) by the end of the study period, suggesting that males and females respond differently to high densities reached in recent years.

This study demonstrates the importance of extreme climatic events as a powerful motor for spread of species in expansion. Also,

it suggests different factors drive emigration of individuals according to their amount of experience in the area (e.g. transients vs residents).

Introduction

Dispersal propensity has major consequences for population structure and dynamics, behavioral ecology and conservation of birds and other organisms [1]. Dispersal can be an adaptive response to environmental changes, or social condition [2]**.** Dispersal also allows an immediate response to unfavorable extreme events such as hurricanes, floods and droughts and is a key element of response to climate change [3,4]. Although research on the effect of extreme events on dispersal dynamics of birds is badly needed [5], this topic has still received little attention from ecologists [6].

Dispersal can be seen as a three-stage movement with emigration, transfer and immigration phases [2]. At the individual level, factors such as status (e.g. age or sex), condition (e.g. body condition, social status), or personality may act as proximate causes of dispersal. For example, juveniles may disperse more than adults because they may have less to lose by moving away [1]. Aggressiveness [7] or individual condition may affect dispersal propensity by changing the ability to compete with conspecifics [8]. At the environmental level, dispersal may be affected by the intrinsic quality of the habitat or by variation of patch quality depending on local resource competition. However, dispersal responses to a given causal factor may vary. For example, dispersal can increase at higher densities as a result of increased competition [9], but it can also decrease at higher density [10,11] owing to conspecific-attraction [12], lower predation risk or Allee effects. Positive and negative density-dependent effects on dispersal can even co-occur in the same population [11,13] demonstrating how the decision to disperse may be affected by other factors. Hence, for a specific population, a positive or negative density effect may depend on being above or below a certain threshold. In newly established bird populations, this

can be tested by studying the relationship between time since colonization and dispersal propensity. Thus, Duckworth and Badyaev [7] found that philopatry increased with time elapsed since colonization in a passerine bird.

The glossy ibis (*Plegadis falcinellus*) is one of the six most widely distributed landbird species [14], and this is probably related to great dispersal ability. It has been suggested that the new World was recently colonized by individuals of this species crossing the Atlantic [15]. Different observations of Doñana born individuals in Barbados (one in autumn 2010), Bermudas (one in autumn 2013) and Trinidad (one in summer 2008) indicate this species can disperse crossing the Atlantic, flying almost 6000 Km away from natal sites (authors unpublished data). The glossy ibis is a migratory and dispersive species with nomadic elements [16], but there have been no previous detailed studies of its dispersal behaviour. At Doñana, seven glossy ibis breeding pairs established in 1996. Since then their number increased quickly to several thousand pairs [17] and Doñana now holds the most important breeding [18] and probably wintering population in western Europe.

The main aim of this study was to test hypotheses about how environmental and individual factors influence the dispersal propensity of a population in expansion, the glossy ibis in Doñana. In the classical mark-recapture multi-site framework [19] longitudinal data from well monitored populations at several locations are used to test hypotheses about the dispersal process (e.g. [20]) of a metapopulation [21]. In the case of glossy ibis, the Doñana and Camargue populations are the only large, well-monitored population, and data from other areas in Europe are sparse. Here, we tested hypotheses about the leaving stage of the dispersal process using a combination of uni-site multievent capture-recapture models [22] on resighting data, and comparison of resightings from within and outside Doñana. We used autumn-to-autumn data because at that

time abundant food was regularly available in Doñana rice-fields, and birds were easier to approach for ring reading. We tested the influence of age and sex as individual factors influencing the dispersal propensity. Furthermore, since dispersal dynamics are strongly related to conditions and individual experience during the breeding season [1], we focused on how environmental conditions during the breeding season may affect the dispersal rate between two consecutive autumns. In particular, we tested how dispersal propensity changes in response to the dramatic changes in population size, annual variation in breeding success and food supplies, and to drought years that make Doñana unsuitable for breeding.

Materials and Methods

Study Area and individual data

Doñana is an extremely important wintering and breeding area for waterbirds [23]. Doñana National park contains about 27000 ha of natural marshes, which provide the main breeding area for glossy ibis [24]. It is surrounded by ca. 36000 ha of rice-fields that provide abundant food to the ibis after harvest [25]. It is characterized by a Mediterranean climate with mild, wet winters and hot, dry summers. Springs in 1999 and 2005 were characterized by extreme local droughts with the flooded surface of natural marshes in June below the 10th percentile of a distribution for the period between 1981 (when remote sensing data were first available for the area) and 2011. This prevented glossy ibis and most waterbirds from breeding at Doñana in these two years. Hereafter we refer to "dry" and "wet" years to distinguish autumns (October - December, the months from which capture - recapture data were obtained) that were followed by spring drought. Therefore, 1998 and 2004 were defined as dry and all the others as wet years. Capture-recapture data in the present study consisted uniquely of resightings. However, for the sake of simplicity, we use the traditional term "trap-happiness" to refer to repeated resightings of the same individual, even though no physical trapping is involved.

Since the establishment of a breeding population of glossy ibis at Doñana (Southwest Spain) in 1996, more than 15000 chicks have been ringed and marked with a darvic ring with an alphanumeric 3-4 digits individual code. These rings may be read with the aid of a telescope from up to 100 meters. Almost 4000 chicks were molecularly sexed (following [26]) and a partially overlapping set of more than 10000 were visually sexed based on tarsus shape [27].

Ringing and blood sampling was approved by Doñana National and Natural Park, Regional Andalusian Government (Consejería de Medio Ambiente), and the Animal Bioethics Committee from Doñana Biological Station. Ringing procedures were approved by the Spanish Ministry of Environment (according to Law 8/2003).

Goodness of Fit

We tested the Goodness of Fit (GOF) of the simple Cormack-Jolly-Seber model separately for birds first resighted in autumn as juveniles or as adults (>1 year old). This approach is conservative as it tests the fit of a more general model with stronger assumptions (i.e. no site or sex differences). The GOF was tested with U-CARE 2.3.3 [28]. The variance inflation factor ($\hat{c}$) was derived from the global test as $\hat{c}=\chi^2/d$, where $\hat{c}>1$ indicates over-dispersion. The global test was statistically significant ($\hat{c}$ = 2 (183.43 / 92); P < 0.001) detecting both a transience effect (of both juveniles and adults) and "trap-happiness" (of juveniles). By "transience effect" we refer to presence of individuals showing up only once in the study area after fledging. Thus, a transience effect can be caused by (*i*) presence of individuals passing through the study area with no chance of returning and / or, (*ii*) by higher mortality rate just after the first resighting. Tavecchia et al. [29], studying Audouin's gull (*Larus audouinii*), showed that many transients dispersed permanently to other areas. On the other hand, "Trap-happiness" of birds first-resighted as juveniles may reflect a lower propensity to temporary emigration in juveniles or a higher fidelity during the first years of life to habitats, like Doñana ricefields, where most of the observations were made. When first encounters were removed, the global test was no longer significant [$\hat{c}$ < 1 (62.98 / 68); P = 0.65; File S1]. As a consequence, we built models by considering a specific parameter type accounting for transience probabilities (we called it "Transience") and included a time-since-marking effect in the global

model, which assigned different probabilities for the first re-encounter of juveniles.

Capture-resighting modeling

We pooled data from October to December, the months in which the majority of observations of marked birds were made. This resulted in 5037 resightings made at Doñana of 3440 individuals observed from 1998 to 2011 (1996 and 1997 were excluded because there were only a handful of marked individuals and they were not sexed). Only sex scores from ringers expert in handling the species were considered in the analyses: of 3440 chicks, 669 (19.4%) were both molecularly and visually sexed, 326 only molecularly sexed, and 1664 only visually sexed. Consequently, we knew with certainty the sex of a portion of individuals, whereas most individuals were visually sexed and therefore subject to error. This uncertainty in sex determination was incorporated into capture-resighting multievent models ([22], File S2) that distinguish what is observed in the field (events) from the underlying biological states.

In this study we considered three states: (*i*) live female, (*ii*) live male, (*iii*) dead or transient (i.e. an individual showing up only once); and four events with the corresponding number used in the data set: (*i*) not seen – "0", (*ii*) seen and visually sexed at birth as female – "1", (*iii*) seen and visually sexed at birth as male – "2", and (*iv*) seen but with sex not determined molecularly nor visually – "3". Multievent models include three parameter types: (*i*) Initial State probabilities, (*ii*) Transition probabilities among states, and (*iii*) Event probabilities conditional on the underlying states.

We set Initial State to be the probability that a bird resighted for the first time was a male. This parameter can be related to the sex ratio of the population at each session if, as in our case, sex had no effect on resighting probabilities and the sampling scheme was not

changed over the study period [30,31]. For simplicity, hereon we will often refer to it as "sex ratio".

The Transition between states referred to the probability of so-called "local mortality" that here we call "apparent dispersal", i.e. the probability that an individual will die or permanently emigrate between t and $t + 1$. This parameter type was broken down into two steps represented by "Transience" and "Residence" matrices. The Transience matrix is related to the probability an individual observed for the first time had of death or permanent emigration before the next autumn, for analogy with apparent dispersal we call it "apparent transience". Hence, the apparent transience probability after the first interval since the first observation is, by definition, zero (details in File S2 and File S5). By contrast, the Residence matrix relates to the apparent dispersal probability of an individual conditional on it being alive and not being a transient after its first interval. Thus, on the one hand the Transience matrix allows estimation of the probability of being a transient (or dying in the first interval). On the other hand, the Residence matrix allows estimation of apparent dispersal of philopatric individuals (residents). For the sake of convenience, hereon we refer to both these parameter types (Transience and Residence) together in combination as unspecified "apparent dispersal" to differentiate it from "apparent dispersal of residents".
Event probabilities were broken down into three steps (Figure 1): (*i*) "Resighting", i.e. the probability of being "resighted", (*ii*) "Visual Sexing", the probability of being visually sexed when first captured at the colony, and (*iii*) "Correctness", the probability of being correctly sexed visually as a female or a male.

We tested the effect of five external covariates on apparent dispersal: (*i*) droughts, (*ii*) breeding success (average n. of fledgings) during the previous and current reproductive seasons ([32], authors unpublished data), (*iii*) population density proxied by breeding population size (see [17]) in the previous spring and (*iv*) food

supplies proxied by the flooded surface in the Guadalquivir marshes in the current spring (June, measured from Landsat images, see [33]). We checked the effects on apparent dispersal of different factors alone, and since drought explained most variation in this parameter, we also tested the effect of the other factors separately on the set of non-drought years. At the individual level, we also tested the effects of age and sex on apparent dispersal.

Model selection

Models were built and fitted to the data using program E-SURGE 1.8.5 [34]. We used the sample-size adjusted Akaike's Information Criterion (AICc) as the model selection criterion [35]. Our model selection procedure was analogous to that proposed by Grosbois and Tavecchia [36]. It aimed to: (*i*) minimize the bias due to the modeling order followed during model selection and, (*ii*) avoid the problematic large number of models arising from considering all the possible combinations of effects and parameter types. In particular, we considered two blocks of parameter types (one for Event, another for Initial State and Transition) and applied a model selection procedure consisting of two different series for each block. In the first series, we modeled each parameter by keeping the others as generalized as possible, in the second we ran models arising from the combinations of the best model structures found in the first series for each parameter (see File S3 for details of the model selection procedure). Hence, we relied mainly on models from series one to test hypotheses, and used models from series two to average parameter estimates [35]. The detailed results from series two are presented in supplementary material (Tables S1, Table S2 and Table S3 in File S4). See File S5 for details of implementation in E-SURGE.

We used the ANODEV procedure [37] to test the hypotheses of the covariate models. This test compares the deviances of the null, the full time-dependent, and the environmental covariate models to

calculate a statistic that follows a Fisher-Snedecor distribution (see [20] for details). The percentage of variation explained by each tested covariate was computed from the deviance of the models, as by Sanz-Aguilar et al. [20]. Spurious effects can be detected when both the parameter to be estimated and the covariate being tested show a linear trend through time ([38], see [39] for an example with density-dependence). Hence, in cases where we detected a trend on a biological parameter, we used the de-trended [40] breeding population size (known to be linearly increasing, [17]) to test for density-dependence.

Apparent dispersal: a good proxy for real dispersal?

As mentioned above, apparent dispersal variation might be due to both true mortality and permanent emigration from the area. Even though we could not ascertain which part of this parameter was due to true mortality and which to permanent emigration, we aimed to test our working-assumption that variation in true dispersal over time was related to variation in "apparent dispersal" over time. To this purpose, we used several different approaches (see next three sections).

Resightings outside Doñana versus apparent dispersal at Doñana

First, we tested for a relationship between the proportion of Doñana glossy ibises resighted outside Doñana the following autumn session and "apparent dispersal". If these parameters (i.e. apparent transience combined with apparent dispersal of residents) varied along with dispersal propensity we would expect to find support for this model. Given that observations outside Doñana are mainly made by amateur bird-watchers, we assumed resighting effort was roughly constant throughout the study period (we excluded observations made by our team in Morocco in 2010). Nonetheless, the number of

observations outside Doñana might depend on changes in population size and not on real changes in dispersal probability. Hence, assuming resighting probability outside Doñana was constant, we used the ratio between the number of resightings outside Doñana and an index of population size (N_{t+1}) for each t + 1 session as a covariate of resighting rate, computed as:

$$N_{t+1} \approx (N_i * 2) + (N_i * bs_i)$$

where N_{ri} and bs_i refer respectively to the number of breeding pairs in Doñana and their breeding success (number of fledgings per pair) at the reproductive season i between t -> t + 1. Then, we tested this effect on apparent dispersal via the models in block two series one (File S3) and tested the significance of the effect according to the ANODEV procedure.

Doñana and Morocco autumn populations

To obtain estimates of dispersal independent of mortality, two teams simultaneously collected resightings over five days (12/11/2010 – 16/11/2010) in Doñana and Morocco (Larache and Souss-Massa) wetlands. Both teams were well trained in reading darvic rings from distance and used the same equipment (20X - 60X zoom telescopes). Thus, we compared the proportion of individuals from each cohort and the total sex ratio of individuals resighted in Doñana and Morocco.

Dispersal range in autumn

We described the dispersal range of Doñana-born glossy ibises based on observations from elsewhere. We used only resightings more than 100 Km away from Doñana and considered the same time intervals (October – December) used in the capture-resighting analyses, plus January since this is the month when extensive efforts are made to count waterbirds during the International Waterbird

Census (IWC) carried out in most range countries. Also, we tested for differences in the proportion of males and females seen at Doñana or elsewhere. Due to sparseness of data, we did not test for sex ratio differences on annual basis but considered only: (*i*) all the autumns pooled together, (*ii*) autumn 2005 (immediately after the last drought) and, (*iii*) from autumn 2005 onwards (when dispersal range appeared to increase).

Results

Capture-resighting analyses

External factors affecting apparent dispersal

Apparent dispersal rates for the two time-intervals comprising a drought were much higher than for the other years. Based on the point estimates ratios, on average apparent transience had 2.5-times higher in dry years whereas the apparent dispersal of residents was 4.0 times higher (Figure 2). Probabilities of apparent transience and apparent dispersal of residents were similar in dry years (0.44, SE = 0.07; 0.49, SE = 0.05, respectively).

For Transience modeling, the model accounting for droughts alone was the most supported and explained 60% of time variation over time ($F_{1,11}$ = 6.65, P = 0.026; model 21-6 in Table 1). Nonetheless, a model accounting for effects of both drought years and breeding success in wet years (*bs*) was selected as the most parsimonious (model 22-2: Table S1 in File S4) in model selection series two (see File S3). Averaged model estimates for apparent transience were computed from this final model selection step (Table S1 in File S4), indicating that the lowest estimate [0.15, (SE = 0.04)] coincided with the highest productivity (in 2009, 2.7 fledgings per pair), and the highest estimate [0.23, (SE = 0.07)] coincided with the lowest productivity (in 2010, 0.87 fledgings per pair) (Figure 2).

The most supported model for Residence modeling (model 21-26 in Table 2) suggested that apparent dispersal of residents was affected by droughts and had a negative linear trend over wet years. The model explained 85% of temporal variation over the whole study period ($F_{2,10}$ = 4.27, P < 0.046). The linear trend effect was marginally significant ($F_{1,9}$ = 4.37, P = 0.066) explaining 49% of apparent dispersal variation in wet years, whose model averaged estimates (Table S1 in File S4) linearly decreased from 0.16 (SE = 0.03) to 0.09 (SE = 0.03) (Figure 2).

In wet years, apparent transience and apparent dispersal of residents were very similar at the beginning of the study period. However, in later years the probability of apparent dispersal of residents decreased consistently, whereas the probability of apparent transience did not show any time-trend throughout the study period (Figure 2).

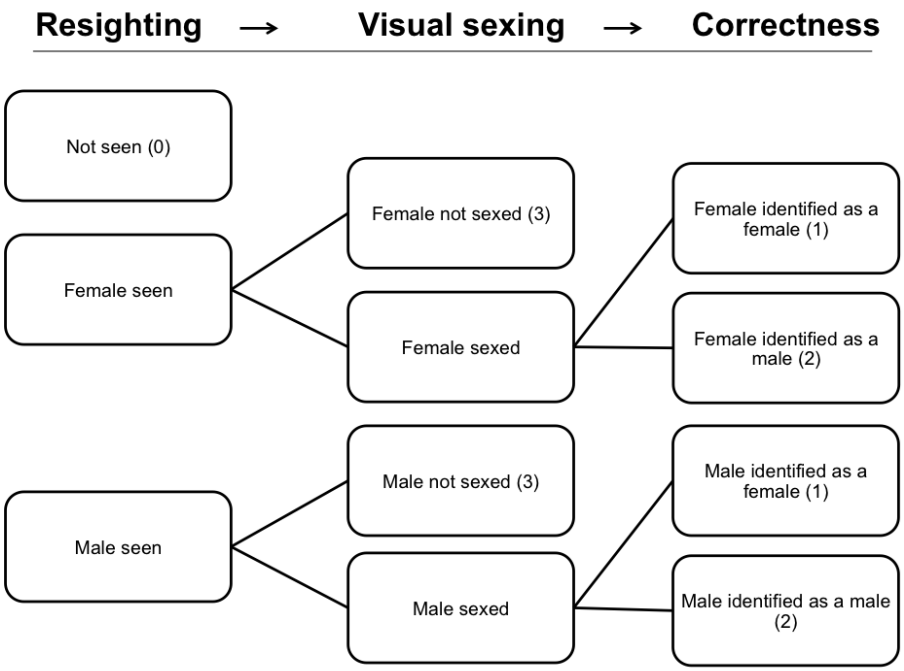

Figure 1. Events and underlying states. The observation process consists of three steps, each one conditional on the event in the previous step. The codes for each event as they appear in the raw data for encounter histories are given in parentheses.

Age and sex differences in apparent dispersal

Apparently, juveniles had slightly higher apparent transience probabilities than adults [model 22 in File S4: Table S2; slope on logit scale = -0.53 (SE = 0.34)]. Nonetheless, 95% confidence intervals of juveniles and adults overlapped (Figure S1 in File S6) and a model without an age effect was also plausible (model 22 *vs.* model 22-2: Table S2 in File S4; ΔAICc = 0.31). Sex was not very influential on

apparent dispersal (Table S2 in File S4). Females had slightly higher apparent dispersal probabilities [Transience, model 23, slope on logit scale = -0.29 (SE = 0.27); Residence, model 25, slope on logit scale = -0.11 (SE = 0.22)] but their 95% confidence intervals overlapped.

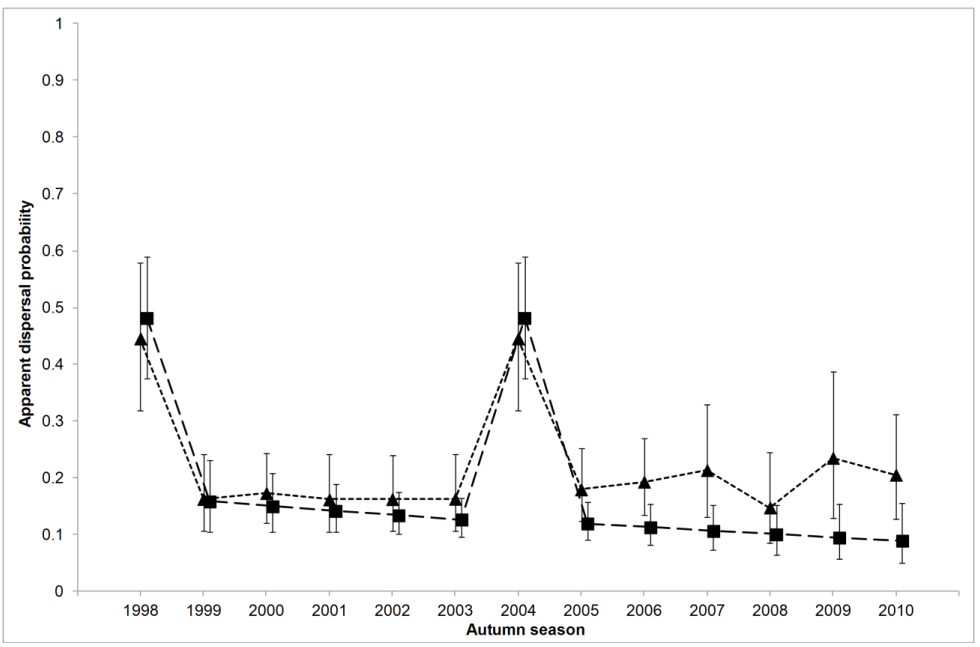

Figure 2. Model averaged estimates of apparent dispersal rates throughout the study period. Apparent dispersal refers to the probability of dying or permanently emigrating from Doñana. Apparent transience (triangles, short-dashed line) was much more pronounced in dry years (1998 and 2004), without any clear trend for other years. Apparent dispersal of residents (squares, long-dashed line) followed a linear decreasing trend over the study period. Estimates and 95%CI are from the model with the lowest AICc (model 22-2 in File S4: Table S1).

Sex ratio

According to Initial State parameter estimates, autumn sex ratio (no. of males / total) at Doñana showed a significant decreasing trend over time (model 21-3 in Table 3; $F_{1,12}$ = 6.42, P = 0.026). Density and droughts had no effect on sex ratio. While at the beginning of the study there was a majority of males (in 1998 0.67, SE = 0.04), by the end there was a majority of females (in 2011 0.44, SE = 0.02) (Figure 3).

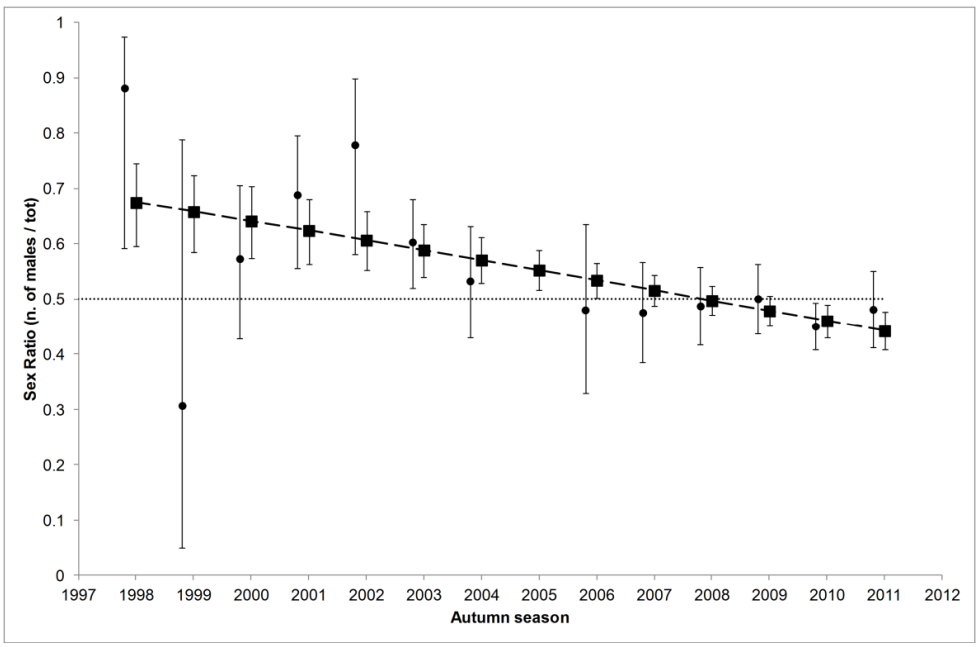

Figure 3. Sex ratio (no. of males over total) of Doñana-born glossy ibises observed in Doñana in autumn. According to the model with lowest AICc (22-2 in Table S1), Initial State estimates (95% CI) switched from a majority of males to a majority of females at the end of the study period (squares, long-dashed line). Circles are estimates (95%CI) from a model with unconstrained time variation (there was no estimate for 2005 due to scarce data). The dotted horizontal line indicates a balanced sex ratio.

Resightings and visual sexing

Resighting probabilities varied among years, showing a general decrease over time probably due to the increase in the number of marked birds alive (Figure S2 in File S6). On average, female chicks were slightly more likely to be visually sexed than males. Both the probability to be visually sexed and its reliability as a sexing method depended on the cohort, with accuracy ranging from 0.80 (SE = 0.03) to 0.99 (SE = 0.005) (Figures S3 and S4 in File S6).

Relationship between real dispersal and apparent dispersal

Resightings elsewhere versus apparent dispersal at Doñana

Apparent transience was positively related to the proportion of resightings outside Doñana corrected for the population size, but this was not the case for apparent dispersal of residents (Transience: $F_{1,11}$ = 6.4, P = 0.028; Residence: $F_{1,11}$ = 0.83, P = 0.38).

Doñana and Morocco autumn populations

Between 12th and 16th November 2010, 417 Doñana-born individuals were resighted in Doñana and 416 in Morocco. The same cohorts (from 2000 to 2010 except 2005) were represented in both areas (Table S3 in File S4).

Of individuals born in 2004, just before the last Doñana drought, 58 were resighted in Morocco and only 7 in Doñana (Chi-square test $c^2_{[1]}$= 35.8, P < 0.01). A higher than expected number of individuals born in 2003 were also recorded in Morocco (Chi-square test $c^2_{[1]}$= 8.3, P < 0.01) while the opposite was found for the 2010 cohort which was relatively more represented in Doñana (Chi-square test $c^2_{[1]}$= 8.3, P < 0.01) indicating a higher presence of very young individuals (8 - 10 months old) at the natal site (Table S3 in File S4). The same proportion of males and females was found in Doñana and Morocco (Chi-square test $c^2_{[1]}$= 0, P = 1; Doñana: n = 87; Morocco: n = 110).

Dispersal range in autumn

The growth of the Doñana population has been associated with an increasing number of observations and resighting locations outside Doñana. The spread to new and more distant areas sharply increased after the 2005 dry year (Figure 4). On average, considering all the autumns together, there was no difference in dispersal between sexes (Chi-square test $\chi^2_{[1]}$= 0.26, n females = 901, n males = 969, P = 0.6); nor was there for the period from 2005 to 2011 (i.e. since the

last drought), (Chi-square test $\chi^2_{[1]} = 2.5$, *n* females = 473, *n* males = 481, *P* = 0.11). On the other hand, a significantly higher proportion of males (16 of 19) than females (8 of 17) dispersed in the drought year 2005 (Chi-square test $\chi^2_{[1]} = 4$, *P* = 0.04).

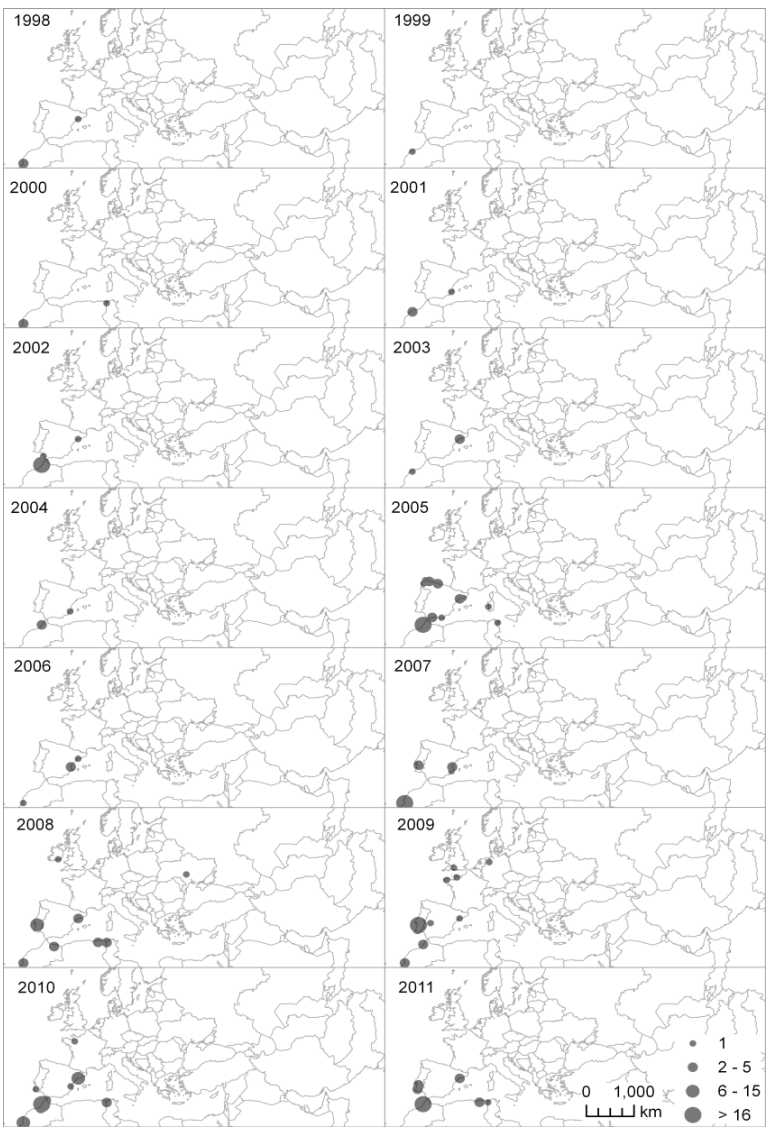

Figure 4. Range expansion according to resightings outside Doñana. Doñana-marked individuals resighted elsewhere for each year throughout the study period (from October to January, records from other months are not shown). Glossy ibises were seen in an increasing number of locations in parallel to the increase in the breeding population in Doñana. A sharp spreading of the population across Europe and northern Africa

occurred during the 2005 drought. An observation from Barbados in September 2010 is not shown.

Discussion

In this study we have found evidence that dispersal rates in a newly established population of glossy ibis changed over time as the population density increased. In a recent evaluation of the conservation state of the glossy ibis in Europe, it was considered of conservation concern in Europe, where it was in decline [41]. However, expansion across Europe and North-west Africa from Doñana is now well underway due to the good reproductive success in most years, transforming the conservation status of the species. However, our study demonstrates how this expansion is largely driven by droughts in Doñana.

Population dynamics

Several studies have focused on the effects of extreme events (like flooding or droughts) on survival and fecundity rates (reviewed in [42]). Nonetheless, other equally important parameters like dispersal or recruitment, crucial for understanding the population responses to extreme events, have scarcely been addressed [6]. Given current changes in climate, there is a critical need for further research on the effects of extreme environmental events on dispersal processes [5]. Droughts can prevent seasonal flooding of wetlands that are crucial for breeding of numerous waterbird species and therefore affect their survival and dispersal rates. Although we cannot rule out an effect on survival, this study demonstrates that glossy ibis dispersal was strongly enhanced by drought events.

We focused on factors affecting two different dispersal strategies: those of individuals present sporadically or regularly (we defined them as transients and residents respectively). Capture-resighting models were built to compute, for each time-interval, the probability of being a transient or dying just after the first resighting and, conditional on being still alive and in the area after the first

interval, the probability of apparent dispersal (i.e. permanently emigrating from the area or dying). In other words, leaving apart the mortality contribution to these probabilities, we dealt with the probability of being a transient and with the emigration probability of residents. Multievent analyses indicated a clear positive effect of droughts on apparent dispersal. Resightings from beyond the study area and analysis on data collected simultaneously in Morocco and Doñana indicated that a drought event (2005) caused a dispersal peak. Moreover, we found strong support for a model relating the proportion of observations from outside with the probability of being transient over the study period. This suggests that apparent transience estimates are strongly related to transient dispersal probabilities over the whole study period, and not just for dry years. However, we did not find similar support for models of the apparent dispersal of residents.

Thus, decreasing apparent dispersal of residents over time (Figure 2) may potentially depend more on changes in true mortality rather than in dispersal propensity. However, we are not confident that this is the case, because illegal shooting at glossy ibis in rice fields and nearby roosting sites may have increased in the area in recent years (personal observation), so we would expect to find an increasing trend in apparent dispersal. On the other hand, it seems more plausible that residents decreased their dispersal propensity over time as they gained experience in the area [43,44].

As a possible outcome of the "win-stay, lose-switch" strategy [45], individuals of any age may cue on their own breeding success and/or those of neighbours to make dispersal decisions [43,46,47]. Hence, breeding failure but also shortage of resources [48,49] might explain why more individuals left the natal area in dry years. However, we did not find strong evidence for a correlation with the surface area of natural marshes that was used as a proxy for available resources (since no direct measure of resources was

available). This may be because this is not a suitable proxy, since for other waterbirds there is evidence that extensive flooding and the associated high water depths lead to a reduction in resource accessibility [50]. Breeding failure owing to drought probably made more ibis individuals permanently emigrate from the area than in other years. In fact, in 2005 a new breeding colony settled in the Camargue wetlands (southern France), [51] and Portugal [52]. Since then several new breeding colonies have been discovered in North Morocco [53], Tunisia [54], Algeria [55] and northern France [56]. A number of Doñana-marked individuals have been observed in these new breeding sites, further suggesting that the Doñana population is fuelling the geographical expansion of the species.

Prospecting behavior in colonial species may serve to gather public information (e.g. breeding success) to help choose the breeding site in the next season [57]. Interestingly, in wet years, transient and resident ibis seemed to follow a different dispersal pattern. Firstly, transient propensity was possibly affected by breeding success at the colony. Although this effect was not significant according to the ANODEV procedure, it received support in terms of AICc in the final step of model selection (File S3; Table S1 in File S4). Several factors may reduce the power of the analysis, like: (*i*) limited time-series data, (*ii*) if most prospecting occurred in the late breeding season (as suggested by Boulinier et al. [57]), this effect may have been overlooked since we focused on individuals observed in the previous autumn, or (*iii*) conditions elsewhere also determine the probability of transients returning to Doñana. Furthermore, prospecting, inexperienced individuals of a colonial species like glossy ibis are more likely to depend on public information (e.g. breeding success) than residents, which are more likely to rely on their own experience (see [43,58]). Secondly, unlike transients, residents decreased their propensity to disperse over time since the species became established in Doñana. The increasing

experience of individuals might favor this process [43,44]. Alternatively, different dispersal phenotypes may have a different fitness according to the time elapsed since colonization, favoring the prevalence of philopatric or disperser phenotypes respectively in recent and long-established populations [59]. Currently, we cannot establish the relative contribution (if any) of these two processes on the apparent increased philopatry of residents.

In general, juvenile birds are expected to be more prone to dispersal [45]. Nonetheless, we did not find a clear effect of age on dispersal propensity. This might be for several reasons: (*i*) under our modeling approach an age effect was tested only on transients (residents by definition were all adults), (*ii*) due to limited sample size we only tested for a difference between individuals one-year old and those of other ages and this may obscure any true correlation, and (*iii*) age might have opposite effects on true mortality and dispersal, counterbalancing each other.

The latter argument can also be applied for the unclear sex effect on apparent dispersal. Nonetheless, the autumn sex ratio of Doñana-born individuals in the natal area was initially strongly male-skewed but this gradually reversed and become female-skewed in the last two years (Figure 3). On the other hand, the sex ratio of chicks at the colony at the moment of marking was balanced except for the last two years when there were more males (unpublished results). Hence, even though more males apparently fledged in those last two years, more females were present during the autumn. This apparent contradiction might be explained if more males than females had dispersed in the last years, a possibility supported from the estimates of a model accounting for the interactive effect of sex and time variation on the apparent dispersal of residents (model 26: Table S2 in File S4; Figure S5 in File S6). We found significantly more males outside Doñana than inside in autumn 2005 (just after the last drought event), suggesting that males and females can use a

different dispersal strategy according to other factors like environmental and demographic conditions. Also, since glossy ibis males are bigger than females [26], they might better withstand moderate levels of competition [60] causing a bias towards males at low density but not at high density when competition increased (Figure 3; Figure S5 in File S6).

Even though density has been found to affect dispersal in many studies [61], we did not find any support for a linear density effect on apparent transience or apparent dispersal of residents. The complexity of density effects with respect to other factors, as discussed above, may explain this result. On the other hand, this might be due to the population size being below a certain threshold above which density-dependent mechanisms start to be effective.

Methodological issues

Single-site capture-resighting models cannot distinguish between true mortality and permanent emigration from the area [62]. Ideally, to separately estimate dispersal and true mortality multi-site models [19] should be applied on longitudinal data collected from several locations covering most of the metapopulation range [20,63]. Nonetheless, logistic and economic limitations often make this unfeasible and longitudinal data are typically available only from one single location where the population has been well monitored. To make multi-site modeling possible, pooling data at broad scales is a common practice but this can magnify survival and re-encounter heterogeneity, hence causing underestimation of sampling variance [64] and biased estimates [65]. Here, we used a single-site approach including specifically designed field-work and showed apparent dispersal mainly reflected dispersal variation [66]. It should be noted that we have only studied permanent emigration probabilities which refer to a one-way movement whereas

movements in both direction are of interest. This represents a shortcoming of our single-site capture-resighting approach. However, our aim was to test hypotheses for the leaving stage of dispersal, not for the transfer and immigration stages [2,36]. Neither did we aim to estimate absolute rates of dispersal or of true mortality.

On the other hand, temporary emigration by ibis is likely to have occurred throughout the study period. Markovian temporary emigration is known to affect the accuracy of transition estimates, but the effect of this bias tend to be small and non-existent when temporary emigration is random [67]. We do not consider that this is a major concern in our study since for testing hypotheses, the focus is on parameter time-variation, which does not require very accurate estimates.

Conclusion

Extreme events are known to affect life-history traits like survival and reproduction [5]. The glossy ibis perfectly illustrates the effects of extreme drought on reproduction as a complete population skipped reproduction in Doñana during drought years. Furthermore, our findings highlight a causal effect between extreme events (like droughts) and dispersal which has been largely overlooked until now. Apart from a negative effect on reproduction, extreme drought episodes have fuelled the expansion of glossy ibis across the Mediterranean region, favoring the establishment of new colonies. These "catastrophic" episodes may be very important drivers in the population dynamics of highly mobile species such as colonial waterbirds. Further research is necessary to clarify the importance of such phenomena on the connectivity and metapopulation dynamics of waterbirds and other highly mobile species.

Acknowledgments

This study has been funded by the projects Ministry of Environment's National Parks research program (Project 028/2002) and by the Regional Government of Andalusia (Junta de Andalucía). SS has been supported by a JAE PhD grant from CSIC (co-funded by the FEDER Program). This study has been possible thanks to the Equipo de Seguimiento de Procesos Naturales that organized the ringing program, especially L.Garcia, M.Mañez, R.Rodriguez, J.L.Arroyo, J.L.delValle and F.Ibañez. We are indebted to all the ornithologists that have contributed observations of marked glossy ibis. R.Baouab made all the arrangements to visit Larache in Morocco. R.Soriguer, M.Vazquez, C.Moreno, L.Gangoso, J.L.Barroso, F.Miranda, C.Perez and many others helped in the ringing and reading of rings at Doñana. We thank A.Sanz-Aguilar, G.Tavecchia, R.Choquet, R.Pradel and an anonymous reviewer for helpful comments on capture-recapture analyses. We are also grateful to J.Kushlan for manuscript reviewing and to D.Aragonés (LAST-EBD) for preparing the map of resightings.

References

1. Clobert J, Baguette M, Benton TG, Bullock JM (2012) Dispersal ecology and evolution. Clobert J, Baguette M, Benton TG, Bullock JM, editors Oxford University Press. Available: http://books.google.es/books?hl=es&lr=&id=wC9qnr4dH5AC&oi=fnd&pg=PP2&dq=dispersal+ecology+and+evolution&ots=o1vK8R4pFh&sig=_8o4y6mC1wpji-_Lsz4m5G_O1Lg. Accessed 9 December 2012.
2. Matthysen E (2012) Multicausality of dispersal: a review. In: Clobert J, Baguette M, Benton TG, Bullock JM, editors. Dispersal Ecology and Evolution. Oxford University Press. pp. 3–18. Available: http://books.google.es/books?hl=es&lr=&id=wC9qnr4dH5AC&oi=fnd&pg=PA3&dq=dispersal+ecology+and+evolution+autor:matthysen&ots=o1vK8R4qFb&sig=cASjiEkoCWtoafZl6NOY50vKlY0. Accessed 9 December 2012.
3. Figuerola J (2007) Climate and Dispersal: Black-Winged Stilts Disperse Further in Dry Springs. PLoS ONE 2: 1–4.
4. Le Galliard JF, Massot M, Clobert J (2012) Dispersal and range dynamics in changing climates: a review. In: Clobert J, Baguette M, Benton TG, Bullock JM, editors. Dispersal Ecology and Evolution. Oxford University Press. pp. 318–336. Available: http://books.google.es/books?hl=es&lr=&id=wC9qnr4dH5AC&oi=fnd&pg=PA317&dq=dispersal+and+range+dynamics+in+changing+climates:+a+review&ots=o1vKbP7qBk&sig=-ECj1erMn_-MCDEgAm-QjgZLnvs. Accessed 12 December 2012.
5. Jenouvrier S (2013) Impacts of climate change on avian populations. Global Change Biology: 1–22. Available: http://doi.wiley.com/10.1111/gcb.12195. Accessed 16 March 2013.
6. Dugger KM, Ainley DG, Lyver PO, Barton K, Ballard G (2010) Survival differences and the effect of environmental instability on breeding dispersal in an Adelie penguin meta-population. Proceedings of the National Academy of Sciences 107: 12375–12380. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2901434&tool=pmcentrez&rendertype=abstract. Accessed 18 March 2013.
7. Duckworth RA, Badyaev A V (2007) Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proceedings of the National Academy of Sciences of the United States of America 104: 15017–15022. Available:

http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1986605&tool=pmcentrez&rendertype=abstract.
8. Barbraud C, Johnson AR, Bertault G (2003) Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition. Journal of Animal Ecology 72: 246–257. Available: http://doi.wiley.com/10.1046/j.1365-2656.2003.00695.x.
9. Negro JJ, Hiraldo F, Donázar JA (1997) Causes of natal dispersal in the lesser kestrel : inbreeding or resource avoidance competition ? Journal of Animal Ecology 66: 640–648.
10. Serrano D, Tella JL, Donázar JA, Pomarol M (2003) Social and individual features affecting natal dispersal in the colonial lesser kestrel. Ecology 84: 3044–3054.
11. Baguette M, Clobert J, Schtickzelle N (2011) Metapopulation dynamics of the bog fritillary butterfly: experimental changes in habitat quality induced negative density-dependent dispersal. Ecography 34: 170–176. Available: http://doi.wiley.com/10.1111/j.1600-0587.2010.06212.x. Accessed 12 December 2012.
12. Smith AT, Peacock MM (1990) Conspecific Attraction and the Determination of Metapopulation Colonization Rates. Conservation Biology 4: 320–323.
13. Kim SY, Torres R, Drummond H (2009) Simultaneous positive and negative density-dependent dispersal in a colonial bird species. Ecology 90: 230–239. Available: http://www.ncbi.nlm.nih.gov/pubmed/19294928.
14. Newton I (2003) The speciation and biogeography of birds. London: Academic Press. Available: http://www.lavoisier.fr/livre/notice.asp?id=OR3WARAL2LAOWF. Accessed 27 August 2012.
15. Patten MA, Lasley GW (2000). Range Expansion of the Glossy Ibis in North America. North american birds, 54, 241–247.
16. Hancock JA, Kushlan JA, Kahl MP (1992) Storks, ibises and spoonbills of the world. San Diego, California: Academic Press Ltd.
17. Santoro S, Mañez M, Green AJ, Figuerola J (2010) Formation and growth of a heronry in a managed wetland in Doñana, southwest Spain. Bird Study 57: 515–524. doi:10.1080/00063657.2010.501371.
18. Figuerola J, Mañez M, Ibáñez F, García L, Garrido H (2004) Morito común Plegadis falcinellus. Libro rojo de las Aves de España. Dirección general para la Biodiversidad. Madrid: SEO/BirdLife. pp. 74–76. Available: http://www.xoriguer.org/ftpdescarregues/libro_rojo_aves_espana.pdf#page=74. Accessed 22 August 2012.
19. Nichols JD, Brownie C, Hines JE, Pollock KH, Hestbeck JB (1993) The estimation of exchanges among populations or

subpopulations. In: Lebreton J, North P, editors. Marked Individuals in the Study of Bird Population. Birkhäuser, Switzerland. pp. 265–279. Available: http://scholar.google.es/scholar?q=The+estimation+of+exchanges+among+populations+or+subpopulations&btnG=&hl=es&as_sdt=0#0. Accessed 20 March 2013.

20. Sanz-Aguilar A, Béchet A, Germain C, Johnson AR, Pradel R (2012) To leave or not to leave: survival trade-offs between different migratory strategies in the greater flamingo. Journal of Animal Ecology 81: 1171–1182. Available: http://www.ncbi.nlm.nih.gov/pubmed/22612528. Accessed 16 July 2012.
21. Hanski I (1998) Metapopulation dynamics. Nature 396: 41–49.
22. Pradel R (2005) Multievent: an extension of multistate capture-recapture models to uncertain states. Biometrics 61: 442–447. doi:10.1111/j.1541-0420.2005.00318.x.
23. Rendón MA, Green AJ, Aguilera E, Almaraz P (2008) Status, distribution and long-term changes in the waterbird community wintering in Doñana, south–west Spain. Biological Conservation 141: 1371–1388.
24. Macías M, Green AJ, Sánchez MI (2004) The Diet of the Glossy Ibis During the Breeding Season in Doñana, Southwest Spain. Waterbirds 27: 234–239.
25. Toral GM, Stillman RA, Santoro S, Figuerola J (2012) The importance of rice fields for glossy ibis (Plegadis falcinellus): Management recommendations derived from an individual-based model. Biological Conservation 148: 19–27. Available: http://linkinghub.elsevier.com/retrieve/pii/S0006320712000936. Accessed 11 March 2012.
26. Griffiths R, Double MC, Orr K, Dawson RJG (1998) A DNA test to sex most birds. Molecular Biology 7: 1071–1075.
27. Figuerola J, García L, Green AJ, Ibáñez F, Mañez M, et al. (2006) Sex determination in glossy ibis chicks based on morphological characters. Ardeola 53: 229–235.
28. Choquet R, Lebreton J-D, Gimenez O, Reboulet A-M, Pradel R (2009) U-CARE: Utilities for Performing Goodness of Fit Tests and Manipulating Capture Recapture Data. Ecography 32: 1–4. Available: http://doi.wiley.com/10.1111/j.1600-0587.2009.05968.x. Accessed 6 March 2012.
29. Tavecchia G, Pradel R, Genovart M, Oro D (2007) Density-dependent parameters and demographic equilibrium in open populations. OIKOS 116: 1481–1492. Available: http://doi.wiley.com/10.1111/j.2007.0030-1299.15791.x. Accessed 5 March 2012.
30. Pradel R (2009) The stakes of Capture-Recapture Models with State Uncertainty. In: Thomson DL, Cooch EG, Conroy MJ,

editors. Modeling Demographic Processes in Marked Populations. New York: Springer. pp. 781–795.
31. Genovart M, Pradel R, Oro D (2012) Exploiting uncertain ecological fieldwork data with multi-event capture-recapture modelling: an example with bird sex assignment. Journal of animal ecology 81: 970–977. Available: http://www.ncbi.nlm.nih.gov/pubmed/22548508. Accessed 4 June 2012.
32. Máñez M, Rendón-Martos M (2009) El morito común , la espátula común y el flamenco común en España . Población en 2007 y método de censo. Máñez M, Rendón-Martos M, editors Madrid: SEO/Birdlife.
33. Kloskowski J, Green AJ, Polak M, Bustamante J, Krogulec J (2009) Complementary use of natural and artificial wetlands by waterbirds wintering in Doñana , south-west Spain. Aquatic Conservation: Marine and Freshwater Ecosystems 19: 815–826. doi:10.1002/aqc.
34. Choquet R, Nogue E (2011) E-SURGE 1.8 user's manual. Montpellier, UMR 5175, France: CEFE.
35. Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York: Springer-Verlag.
36. Grosbois V, Tavecchia G (2003) Modeling dispersal with capture – recapture data : disentangling decisions of leaving and settlement. Ecology 84: 1225–1236.
37. Skalski JR, Hoffmann A, Smith SG (1993) Testing the significance of individual-and cohort-level covariates in animal survival studies. In: Lebreton JD, North PM, editors. Marked Individuals in the Study of Bird Population. pp. 9–28. Available: http://scholar.google.es/scholar?q=Testing+the+significance+of+individual+and+covariates+in+animal+survival&hl=es&as_sdt=0&as_ylo=1990&as_yhi=#0. Accessed 23 November 2012.
38. Grosbois V, Gimenez O, Gaillard J-M, Pradel R, Barbraud C, et al. (2008) Assessing the impact of climate variation on survival in vertebrate populations. Biological Reviews 83: 357–399. Available: http://www.ncbi.nlm.nih.gov/pubmed/18715402. Accessed 30 October 2012.
39. Coulson JC (2001) Does density-dependent mortality occur in wintering Eurasian Oystercatcher Haematopus ostralegus and breeding adult Black-legged kittiwakes Rissa tridactyla? Ibis 143: 500–502.
40. Graham MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology 84: 2809–2815.
41. Delany S, Scott D (2006) Waterbird Population Estimates. WagenIngen, Netherlands: Wetlands International 202.

42. Moreno J, Møller AP (2011) Extreme climatic events in relation to global change and their impact on life histories. Current Zoology 57: 375–389.
43. Serrano D, Tella JL, Forero MG, Donázar JA (2001) Factors affecting breeding dispersal in the facultatively colonial lesser kestrel : individual experience vs. conspecific cues. Journal of Animal Ecology 70: 568–578.
44. Balkiz Ö, Béchet A, Rouan L, Choquet R, Germain C, et al. (2010) Experience dependent natal philopatry of breeding greater flamingos. Journal of Animal Ecology 79: 1045–1056.
45. Switzer P V (1993) Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7: 533–555. Available: http://www.springerlink.com/content/g5h624m730762894/. Accessed 20 November 2011.
46. Danchin E, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79: 2415–2428.
47. Roche EA, Gratto-Trevor CL, Goossen JP, White CL (2012) Flooding Affects Dispersal Decisions in Piping Plovers (Charadrius melodus) in Prairie Canada. The auk 129: 296–306.
48. Bonte D, Lukáč M, Lens L (2008) Starvation affects pre-dispersal behaviour of Erigone spiders. Basic and Applied Ecology 9: 308–315. Available: http://linkinghub.elsevier.com/retrieve/pii/S1439179107000278. Accessed 16 March 2013.
49. Mathieu J, Barot S, Blouin M, Caro G, Decaëns T, et al. (2010) Habitat quality, conspecific density, and habitat pre-use affect the dispersal behaviour of two earthworm species, Aporrectodea icterica and Dendrobaena veneta, in a mesocosm experiment. Soil Biology and Biochemistry 42: 203–209. Available: http://linkinghub.elsevier.com/retrieve/pii/S0038071709003952. Accessed 5 March 2013.
50. Almaraz P, Green AJ, Aguilera E, Rendón MA, Bustamante J (2012) Estimating partial observability and nonlinear climate effects on stochastic community dynamics of migratory waterfowl. Journal of animal ecology 81: 1113–1125. Available: http://www.ncbi.nlm.nih.gov/pubmed/22372885. Accessed 23 May 2013.
51. Kayser Y, Gauthier-Clerc M, Paz L, Balleteros M, Baudouin S, et al. (2006) Nouveaux cas de nidification de l'Ibis falcinelle Plegadis falcinellus en Camargue en 2006. Ornithos 13: 322–325. Available: http://scholar.google.es/scholar?hl=es&q=Nouveaux++cas+de+nidification+de+l'Ibis+falcinelle++Plegadis+falcinellus+en+Camargue+en+2006&btnG=&lr=#0. Accessed 9 December 2012.
52. Noivo C, Jara J (2007) First records of breeding Glossy Ibis Plegadis falcinellus in Portugal. Anuario Ornitologico 5: 133–135.

53. Amezian M, Khamlichi R El, Elbanak A (2012) Breeding of Glossy Ibis Plegadis falcinellus in the mixed heronry adjacent to Smir marshes, northern Morocco. Alauda 80: 33–38. Available: http://moroccanbirds.webs.com/Publications/Amezian et al 2012_Plegadis falcinellus.pdf. Accessed 9 December 2012.
54. Nefla A, Ouni R, Nouira S (2012) The Breeding Status of the Glossy Ibis Plegadis falcinellus in the Lebna Dam in Cap Bon , Tunisia. Journal of Life Sciences 6: 776–782.
55. Boucheker A, Nedjah R, Samraoui F, Menaï R, Samraoui B (2009) Aspects of the Breeding Ecology and Conservation of the Glossy Ibis in Algeria. Waterbirds 32: 345–351. Available: http://www.bioone.org/doi/abs/10.1675/063.032.0215. Accessed 9 December 2012.
56. Marion L, Marion P (2011) Première reproduction prouvée de l'Ibis falcinelle Plegadis falcinellus au lac de Grand-Lieu (Loire-Atlantique). Alauda 79: 215–219. Available: http://cat.inist.fr/?aModele=afficheN&cpsidt=24515795. Accessed 9 December 2012.
57. Boulinier T, Danchin E, Monnat J-Y, Doutrelant C, Cadiou B (1996) Timing of prospecting and the value of information in a colonial breeding bird. Journal of Avian Biology 27: 252–256.
58. Kim SY, Torres R, Rodriguez C, Drummond H (2007) Effects of breeding success, mate fidelity and senescence on breeding dispersal of male and female blue-footed boobies. J Anim Ecol 76: 471–479.
59. Duckworth RA (2008) Adaptive dispersal strategies and the dynamics of a range expansion. The American naturalist 172 Suppl : S4–17. Available: http://www.ncbi.nlm.nih.gov/pubmed/18554143. Accessed 14 March 2013.
60. Hanski I, Peltonen A, Kaski L (1991) Natal dispersal and social dominance in the common shrew Sorex araneus. Oikos 62: 48–58. Available: http://www.jstor.org/stable/10.2307/3545445. Accessed 12 December 2012.
61. Matthysen E (2005) Density-dependent dispersal in birds and mammals. Ecography 28: 403–416.
62. Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62: 67–118.
63. Schaub M, Ullrich B, Knötzsch G, Albrecht P, Meisser C (2006) Local population dynamics and the impact of scale and isolation : a study on different little owl populations. Oikos 115: 389–400.
64. Anderson DR, Burnham KP, White GC (1994) AIC model selection in overdispersed capture-recapture data. Ecology 75: 1780–1793.

65. Pollock KH, Nichols JD, Brownie C, Hines JE (1990) Statistical inference for capture-recapture experiments. Wildlife monographs 107: 3–97. Available: http://www.jstor.org/stable/10.2307/3830560. Accessed 6 May 2013.
66. Pakanen V-M, Hildén O, Rönkä A, Belda EJ, Luukkonen A, et al. (2011) Breeding dispersal strategies following reproductive failure explain low apparent survival of immigrant Temminck's stints. Oikos 120: 615–622. Available: http://doi.wiley.com/10.1111/j.1600-0706.2010.18953.x. Accessed 12 March 2013.
67. Kendall WL, Nichols JD (2002). Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. Ecology, 83(12), 3276–3284.

Tables

Table 1. Multievent modeling of apparent transience (Transience matrix) of glossy ibises related to external covariates.

Model	Transients dispersal	*np*	Dev	AICc	ΔAICc	*wi*	$F_{1,11}/F_{2,10}$	*P*-value	*F*1,9	P-value	R^2_{tot}	R^2_{wet}
21-6	Dry years	68	16028.50	16166.39	0.00	0.30	6.65	0.026			0.60	
21-15	Dry years, *bs* on wet years	69	16027.45	16167.39	1.00	0.18	3.22	0.080	0.94	0.360	0.64	0.10
21-17	Dry years, *fgm* on wet years	69	16028.11	16168.06	1.67	0.13	3.10	0.090	0.35	0.570	0.62	0.04
21-14	Dry years, *dens* on wet years	69	16028.26	16168.20	1.81	0.12	3.07	0.090	0.22	0.650	0.61	0.02
21-13	Dry years, *T* on wet years	69	16028.45	16168.39	2.00	0.11	3.03	0.090	0.05	0.830	0.61	0.01
21-16	Dry years bs_{t-1} on wet years	69	16028.48	16168.43	2.04	0.11	3.03	0.090	0.02	0.890	0.61	0.00
21-9	*bs*	68	16032.17	16170.05	3.66	0.05	5.11	0.046			0.46	
21-gm	*T*	78	16018.10	16176.58	10.19	0.00						
21-12	Dry years, *t* on wet years	78	16018.42	16176.90	10.51	0.00						
21-11	*fgm*	68	16041.33	16179.22	12.83	0.00	1.28	0.280			0.12	
21-5	*Constant*	67	16044.39	16180.22	13.83	0.00						
21-10	*bs0*	68	16043.98	16181.87	15.48	0.00	0.17	0.690			0.02	
21-8	*dens*	68	16044.11	16182.00	15.61	0.00	0.12	0.740			0.01	
21-7	*T*	68	16044.38	16182.27	15.88	0.00	0.00	0.960			0.00	

Model notation: np, number of estimable parameters; Dev, relative deviance; AICc, Akaike information criterion corrected for small sample size; ΔAICc, the AICc difference of the current model with respect to the lowest AICc value; w_i, Akaike's weight, *F*1,11 / *F*2,10, F-statistic computed for the whole period of study, number of d.f. depends on the current model; *F*1,9, F-statistic computed for the wet years; R^2_{tot}, current model percentage of variation explained over the whole study period; R^2_{wet}, current model percentage of variation explained over the wet years; *bs*, breeding success (nº of fledgings per pair) for the reproductive season between autumn seasons bs_{t-1}, breeding success in the last reproductive season; *dens*, population size in the last breeding season; *fgm*, flooded surface of natural marshes in Doñana National Park in June; *T*, linear trend; *t*, unspecific time variation. All the models were run with unspecific time variation on Initial State and Residence and the best ranked structure for the resighting parameter types (Event).

Table 2. Multievent modeling of apparent dispersal of residents (Residence matrix) of Doñana glossy ibises related to external covariates

Model	Transients dispersal	*np*	Dev	AICc	ΔAICc	*wi*	$F_{1,11}$ / $F_{2,10}$	*P*-value	*F*1,9	P-value	R^2_{tot}	R^2_{wet}
21-26	Dry years, *T* on wet years	70	16022.96	16164.96	0.00	0.54	4.27	0.046	4.37	0.066	0.85	0.49
21-19	Dry years	69	16027.46	16167.40	2.45	0.16	7.90	0.017			0.72	
21-28	Dry years, *bs* on wet years	70	16026.50	16168.50	3.54	0.09	3.73	0.062	0.93	0.430	0.75	0.10
21-27	Dry years, *dens* on wet years	70	16026.50	16168.50	3.55	0.09	3.73	0.062	0.93	0.360	0.75	0.10
21-30	Dry years, *fgm* on wet years	70	16027.18	16169.18	4.22	0.06	3.63	0.065	0.27	0.660	0.73	0.03
21-29	Dry years *bs0* on wet years	70	16027.45	16169.46	4.50	0.06	3.59	0.067	0.01	0.920	0.72	0.00
21-gm	*T*	78	16018.10	16176.58	11.63	0.00						
21-25	Dry years, *t* on wet years	78	16018.18	16176.67	11.71	0.00						
21-22	*bs*	69	16039.72	16179.66	14.71	0.00	3.83	0.076			0.35	
21-23	*bs0*	69	16048.29	16188.23	23.27	0.00	0.99	0.340			0.09	
21-18	*Constant*	68	16051.28	16189.17	24.21	0.00						
21-24	*fgm*	69	16049.70	16189.65	24.69	0.00	0.52	0.490			0.05	
21-21	*dens*	69	16050.28	16190.22	25.26	0.00	0.33	0.580			0.03	
21-20	*T*	69	16051.28	16191.22	26.26	0.00	0.00	0.970			0.00	

Model notation: as in the Table 1. All the models were run with unspecific time variation on Initial State and Transience and best ranked structure for the resighting parameter types (Event).

Table 3. Multievent modeling of Doñana autumn sex ratio (Initial State parameter) of native glossy ibises related to external covariates

Model	Transients dispersal	*np*	Dev	AICc	ΔAICc	*wi*	*F*1,11 / *F*2,10	*P*-value	R^2_{tot}
21-3	*T*	66	16033.44	16167.22	0.00	1	6.42	0.026	0.54
21-gm	*t*	78	16018.10	16176.58	9.37	0.00			
21-1	*Constant*	65	16051.09	16182.82	15.60	0.00			
21-2	Dry years	66	16049.88	16183.66	16.44	0.00	0.44	0.520	0.04
21-4	*dens*	66	16050.81	16184.59	17.38	0.00	0.10	0.760	0.01

Model notation: as in the Table 1 legend. All the models were run with unspecific time variation on Transience and Residence and the best ranked structure for the resighting parameter types (Event).

Supporting Information

File S1. Goodness-of-fit results.

BEFORE SUPPRESSION OF FIRST ENCOUNTER:

Global TEST, number of groups =2 (Captured as juveniles, captured as adults)
df =92
Quadratic Chi2 =183.4267
   ->P-level=4.8508e-008
N(0,1) statistic for transient(>0) =6.6833
   ->P-level, two-sided test =2.3362e-011
   ->P-level, one-sided test for transience =1.1681e-011
N(0,1) signed statistic for trap-dependence =-2.7123
   ->P-level, two-sided test =0.0066813

TEST3.SR, group 1 = Captured as juveniles
N(0,1) statistic for transient(>0) =5.6269
   P-level, two-sided test =1.8344e-008
   P-level, one-sided test for transience =9.172e-009
****

TEST3.SR, group 2 = Captured as adults
N(0,1) statistic for transient(>0) =3.7834
   P-level, two-sided test =0.00015467
   P-level, one-sided test for transience =7.7337e-005
****

TEST2.CT, group 1 = Captured as juveniles
N(0,1) signed statistic for trap-dependence =-3.4311
trap-happiness<0   trap-shyness>0
   P-level, two-sided test =0.00060114
****

TEST2.CT, group 2 = Captured as adults
N(0,1) signed statistic for trap-dependence =-0.15665
trap-happiness<0   trap-shyness>0
   P-level, two-sided test =0.87552
****

AFTER SUPPRESSION OF FIRST ENCOUNTER:

Global TEST, number of groups =2 (Captured as juveniles, captured as adults)

df =68
Quadratic Chi2 =62.9805
->P-level=0.64948
N(0,1) statistic for transient(>0) =0.37264
->P-level, two-sided test =0.70941
->P-level, one-sided test for transience =0.35471
N(0,1) signed statistic for trap-dependence =-1.0815
->P-level, two-sided test =0.27949

TEST3.SR, group 1 = Captured as juveniles
N(0,1) statistic for transient(>0) =0.24878
P-level, two-sided test =0.80353
P-level, one-sided test for transience =0.40177
****

TEST3.SR, group 2 = Captured as adults
N(0,1) statistic for transient(>0) =0.28257
P-level, two-sided test =0.77751
P-level, one-sided test for transience =0.38876
****

TEST2.CT, group 1 = Captured as juveniles
N(0,1) signed statistic for trap-dependence =-1.6623
trap-happiness<0 trap-shyness>0
P-level, two-sided test =0.096452
****

TEST2.CT, group 2 = Captured as adults
N(0,1) signed statistic for trap-dependence =0.30148
trap-happiness<0 trap-shyness>0
P-level, two-sided test =0.76305

File S2. Multievent probabilistic framework of the study.

Multievent models combine information from events with the underlying states to estimate probabilities of several parameters. A multievent model accounts for three parameter types: Initial State, State Transition and Event probabilities.
In this study we defined three underlying biological states:
† - Death or transient (referring to the state with zero probability of resighting due to its permanent emigration from the study area or to being dead)
♀ - Female alive at Doñana
♂ - Male alive at Doñana

The events, numbered as they appear in the data set, were four:
0 - Bird not resighted
1 - Bird resighted, visually identified as female when it was a chick
2 - Bird resighted, visually identified as male when it was a chick
3 - Bird resighted, not sexed visually when it was a chick

INITIAL STATE
This parameter refers to the probability that, when an individual is first resighted at Doñana in autumn, it is a male. Thus, assuming (*i*) there are no differences between p of resighting of males and females and (*ii*) the sampling scheme has not varied during the study period, this parameter is related to the sex ratio of the population [1, 2] of Doñana-born individuals at their natal site in autumn. By definition, the probability of being first captured as death or transient is zero. Therefore, the initial state probabilities are:

♀	♂
1-π	π

π is the probability that, when an individual is first resighted at Doñana in autumn, it is a male.

STATE TRANSITION
This parameter type was divided in two steps. These probabilities are best represented in the form of stochastic matrices with departure

states in rows and arrival states in columns. Transitions between genders were not allowed.

Step 1 - Transience; this step computes the probability that an individual first resighted on occasion *t* dies or permanently emigrates from the area in the interval between *t* and *t* + 1. As a consequence, it only applies for this interval (see below Additional file 5 for details on implementation in E-SURGE).

	♀	♂	†
♀	$1-\varphi_f$	0	φ_f
♂	0	$1-\varphi_m$	φ_m
†	0	0	1

Where φ_f and φ_m refer respectively to the probability a female or a male has of permanently emigrating or dying in the interval after its first resighting.

Step 2 - Residence (conditional on Transience); this step computes the probability a non-transient (i.e. one individual still available to be resighted after its first resighting) has of dying or permanently emigrating from the area between *t* and *t* + 1 (ψ_f for a female and ψ_f for a male).

	♀	♂	†
♀	$1-\psi_f$	0	ψ_f
♂	0	$1-\psi_m$	ψ_m
†	0	0	1

The notation is the same used for the step 1.

EVENT

The Event probabilities relate the events to the underlying biological states. This parameter type has been divided into three steps.

Step 1 - Resighting; This estimates the probability (β_f and β_m for a female and male respectively) one individual has to be resighted at *t* + 1.

	not seen	live ♀ seen	live ♂seen
♀	$1 - \beta_f$	β_f	0
♂	$1 - \beta_m$	0	β_m
†	1	0	0

Same notation as above.

Step 2 - Visual Sexing (conditional on Resighting); this estimates, conditional on being resighted, the probability (γ_f and γ_m for a female and male respectively) one individual has to be visually sexed when it was a chick.

	not seen	not sexed	live ♀ sexed	live ♂sexed
not seen	1	0	0	0
live ♀ seen	0	$1 - \gamma_f$	γ_f	0
live ♂seen	0	$1 - \gamma_m$	0	γ_m

Same notation as above

Step 3 - Correctness (conditional on Resighting and Visual Sexing); This estimates, conditional on being resighted and visually sexed, the probability (δ_f and δ_m for a female and a male respectively) an individual has of being correctly visually sexed as a female or a male.

	0	1	2	3
not seen	1	0	0	0
not sexed	0	0	0	1
live ♀ sexed	0	δ_f	0	$1 - \delta_f$
live ♂sexed	0	0	δ_m	$1 - \delta_m$

Same notation as above

References:

1. Pradel R: **The stakes of Capture-Recapture Models with State Uncertainty**. In *Modeling Demographic Processes in Marked Populations*. Edited by Thomson DL, Cooch EG, Conroy MJ. New York: Springer; 2009:781–795.

2. Genovart M, Pradel R, Oro D: **Exploiting uncertain ecological fieldwork data with multi-event capture-recapture modelling: an example with bird sex assignment.** *Journal of animal ecology* 2012, **81**:970–977.

File S3. Model selection procedure.

Model selection procedure

Given the high number of biological parameters, we divided the analysis into two blocks, each one with two series: in block 1 we modeled Resighting, Visual sexing and Correctness, and in block 2 we modeled Initial State, Transience and Residence. In series 1 (Table 1, Table 2, Table 3 and Table S4) we modeled each biological parameter by keeping the others as general as possible and in series 2 (Table S1 and Table S5) we ran all the possible combinations of models which resulted to be within 2 ΔAICc in series 1. Thus, for each block we reached a supposed best model we named *bm1* (block 1, Table S5) and *bm2* (block 2, Table S1).

In block 1, we tested the trap-dependence effect on Resighting (sex effect was discarded by a preliminary analysis), and cohort and gender effects on Visual Sexing and Correctness. In the block 2, we tested several hypotheses concerning the possible effects of extrinsic factors on the sex ratio and both the apparent transience and residents apparent dispersal. All the tested covariates were standardized [1]. De-trended values of population abundance were used to test for density effects on residents apparent dispersal, since a significant linear effect (according to ANODEV) was found for this parameter type (details are given in the Methods section).

When modeling block 2, the structure of Event parameters was kept the same as for *bm1*, while the effects of age and gender on Transience and Residence were not tested. We specifically tested these effects on *bm2* (Table S2). The age effect was tested only on Transience because a non-transient individual apparent dispersal probability (hence modeled in Residence) was the same as for adults. Model averaging estimates [2] for Transition parameters were

computed from all the models in block 2 series 2 (Table S1). All the other estimates proceed from *bm2*.

References:

1. Choquet R, Nogue E: *E-SURGE 1.8 User's Manual*. Montpellier, UMR 5175, France: CEFE; 2011(September).
2. Burnham KP, Anderson DR: *Model Selection and Multimodel Inference: a Practical Information-theoretic Approach*. 2nd ed. New York: Springer-Verlag; 2002.

File S4. Supplementary tables.

Contains: **Table S1. Set of candidate models used to model average apparent dispersal estimates**; **Table S2. Age and sex effects on apparent dispersal probabilities**; **Table S3. Cohorts of marked individuals resighted at Doñana or in Morocco between 12th and 16th December 2010**; **Table S4. Set of candidate models from initial Event modeling (block 1 series 1)**; and **Table S5. Set of candidate models from final Event modeling (block 1 series2)**.

Table S1. The candidate set of models for block 2 series 2. We computed model averaged apparent dispersal estimates from this set of models. We ran all the combinations of effects found to be within 2 AICc units from the best model for each biological parameter (Transience, Residence and Initial State, see Table 1, 2 and 3). Model notation: as in Table 1, between parentheses are the effects considered on Initial State (IS), Transience (T) and R (Residence). The model in bold has the lowest AICc and hence represents the *bm2*.

Model	Model structure	*np*	Dev	AICc	ΔAICc	w_i
22-2	**IS[Trend] T[Dry years + *bs*] R[Dry years + Trend]**	**48**	**16064.61**	**16161.55**	**0.00**	**0.62**
22-1	IS[Trend] T[Dry years] R[Dry years + Trend]	47	16068.71	16163.62	2.07	0.22
22-4	IS[Trend] T[Dry years + *dens*] R[Dry years + Trend]	48	16068.64	16165.58	4.03	0.08
22-3	IS[Trend] T[Dry years + *fgm*] R[Dry years + Trend]	48	16068.69	16165.63	4.08	0.08

Table S2. Multievent modeling of apparent transience and apparent dispersal of residents of Doñana glossy ibises related to age and sex effects. Age was tested only on apparent transience probability given that residents were all adults by definition. Model notation: as in Table S1, "T" refers to apparent transience and "R" refers to apparent dispersal of residents. Age was tested only as an addictive effect whereas sex was tested as an additive effect "Sex (+)", or as an interactive effect "Sex (*)".

Model	Model structure	*np*	Dev	AICc	T ΔAICc	R ΔAICc	Tw_i	Rw_i
22-2	No effect	48	16064.61	16161.55	0.31	0.01	0.32	0.45
21	Age and Sex (+) on Transients	50	16062.02	16163.05	1.80		0.15	
22	Age on Transients	49	16062.26	16161.24	0.00		0.37	
23	Sex (+) on Transients	49	16064.29	16163.27	2.03		0.14	
24	Sex (*) on Transients	51	16063.57	16166.63	5.39		0.03	
25	Sex (+) on Residents	49	16062.56	16161.54		0.00		0.45
26	Sex (*) on Residents	51	16061.50	16164.56		3.02		0.10

Table S3 Number of individuals from each cohort, resighted at Doñana or in Morocco between 12th and 16th December 2010.

Site	Cohorts										n
	2000	2001	2002	2003	2004	2006	2007	2008	2009	2010	
Doñana	3	1	4	3	7	15	40	37	104	203	417
Morocco	1	7	12	17	58	14	33	45	91	138	416

Table S4 Block 1 series 1 model selection. At this stage, the global model structure was held for all the Transition and Initial State parameters while the Event parameters were modeled one-by-one by keeping the other two fixed as from the global model. Hence, models 1_1 to 1_3 aimed to find the best structure for Resighting, models 1_1, 1_4, 1_5 for Visual Sexing, and models 1_1, 1_6, 1_7 for Correctness. Model notation: R, Resighting (parameter type); VS, Visual Sexing; C, Correctness; trap.tt, trap effect with individuals resighted at the next session from their first resighting having a time-varying p of encounter different from the p of being resighted at subsequent sessions (which was also time-varying); trap.t+t, the same as trap.tt but the p values at subsequent sessions were additively time-varying with respect to the p values at the second session from the first resighting; t, time varying; sex, sex effect; cohort, birth-year effect. Irrelevant models such as those assuming constant time effect on Resighting are not reported here.

Model	Structure	np	Deviance	ΔICc	R - ΔAICc	VS - ΔAICc	C - ΔAICc
11-1	R {trap.tt} VS{sex+cohort} C{sex+cohort}	96	15997.98	16193.75	9.56	0.00	0.85
11-2	R{trap.t+t} VS{sex+cohort} C{sex+cohort}	85	16011.35	16184.31	0.12		
11-3	R{t} VS{sex+cohort} C{sex+cohort}	84	16013.30	16184.19	0.00		
11-4	R{trap.tt} VS{sex} C{sex+cohort}	83	17110.70	17279.51		1085.77	
11-5	R{trap.tt} VS{cohort} C{sex+cohort}	95	16023.07	16216.76		23.01	
11-6	R{trap.tt} VS{sex+cohort} C{sex}	85	16106.24	16279.19			86.30
11-7	R{trap.tt} VS{sex+cohort} C{cohort}	95	15999.21	16192.90			0.00

Table S5 Block 1 series 2 model selection. At this stage we run all the models arising from all the combinations of effects found to be within 2 ΔAICc from the best model for each parameter type modeled in Block 1 series 1. The Event structure as from the lowest AICc model found (*bm1*) at this stage was retained for modeling in Block 2. Model notation as from Table S4.

Model	Structure	np	Deviance	AICc	ΔAICc
12-1 (*bm1*)	R{t} VS{sex+cohort} C{cohort}	83	16014.545	16183.3603	0
12-2	R{t} VS{sex+cohort} C{sex+cohort}	84	16013.3019	16184.1856	0.8253
12-3	R{trap.t+t} VS{sex+cohort} C{cohort}	84	16012.5737	16183.4574	0.0971
12-4	R{trap.t+t} VS{sex+cohort} C{sex+cohort}	85	16011.3322	16184.2851	0.9248

File S5. Implementation in E-SURGE.

The data set was prepared according to the "HEADED format" [1]. Once E-SURGE was launched, the data set was loaded and divided into covariate-groups according to (*i*) molecular sex, (*ii*) age at first resighting, and (*iii*) cohort. Thus, 84 groups were defined according to birth-year (14 cohorts), age (juvenile or adult) at first resighting and molecular sex (female, male or unknown).

Then, in "Data Input / Modify" the number of states were reduced from four to three, the number of events was left equal to four and the number of age classes was reduced to two (instead of 13 available).

In "Advanced Numerical / Modify", to improve results precision and facilitate convergence, we diminished the tolerance to parameter change to 1e-008 [1]. To reduce possibility of convergence on a false (local) minimum, we set "Advanced Numerical / Initial Values" to Multiple Random (= 5).

Afterwards, in "COMPUTE A", in this order we:

1) Loaded the GEPAT structure:

```
%%%% VERSION 2.0 %%%%%%%
3
%%%% Initial state %%%%%%%
1
1 2  IS
* P
%%%% Transition %%%%%%%
2
3 3  Transience
* - p
- * p
- - *
3 3  Residence
* - p
```

- * p
- - *
%%%% Event %%%%%%
3
3 3 Resighting
* b -
* - b
* - -
3 4 Visual Sexing
* - - -
- * p -
- * - p
4 4 Correctness
* - - -
- - - *
- p * -
- * p -

2) Defined the GEMACO structure for the current model. The GEMACO structure of the global model was:
For Initial State: IS - Step 1 - (16): fem+mal+unk.t
For Transition: Transience - Step 1: a(1).[edad+f+t]+a(2)
For Transition: Residence - Step 2: f+t
For Event: Resighting - Step 1:
firste+[nexte.[captjuv.a(2)].t]+[nexte.[[captjuv.a(3)]&captad].t]
For Event: Visual Sexing - Step 2: birthyear+f
For Event: Correctness - Step 3: f+birthyear
Where these shortcuts were used:
"fem" = "molecularly sexed as females",
"mal" = "molecularly sexed as males",
"unk" = "molecularly unsexed ",
"edad" = "first resighting as juvenile vs first resighting as adult",
"captjuv" = "first time resighted being a juvenile",
"captad" = "first time resighted being an adult",

"birthyear" = "birth-year"

3) Set the IVFV:

For the Initial State, the probability of "fem" to be initially resighted as a male was fixed to zero and that of "mal" to one. For the "Transition - Step 1" the last parameter, corresponding to a(2) was set to zero since Transience by definition must apply only to the interval after first resighting. For "Event - Step 1", as usual, the first parameter was set to one because it refers to the probability of resighting for the first resighting of any individual.

4) RUN

References

1. Choquet R, Nogue E: *E-SURGE 1.8 User's Manual*. Montpellier, UMR 5175, France: CEFE; 2011(September).

File S6. Supplementary figures.

Contains: **Figure S1. Apparent transience probabilities according to age and time; Figure S2. Resighting probabilities**; **Figure S3. Visual sexing probabilities for ring-marked chicks**; **Figure S4. Yearly probabilities of correct visual sexing for ringed-marked chicks**; **Figure S5. Apparent dispersal probabilities of residents according to sex**.

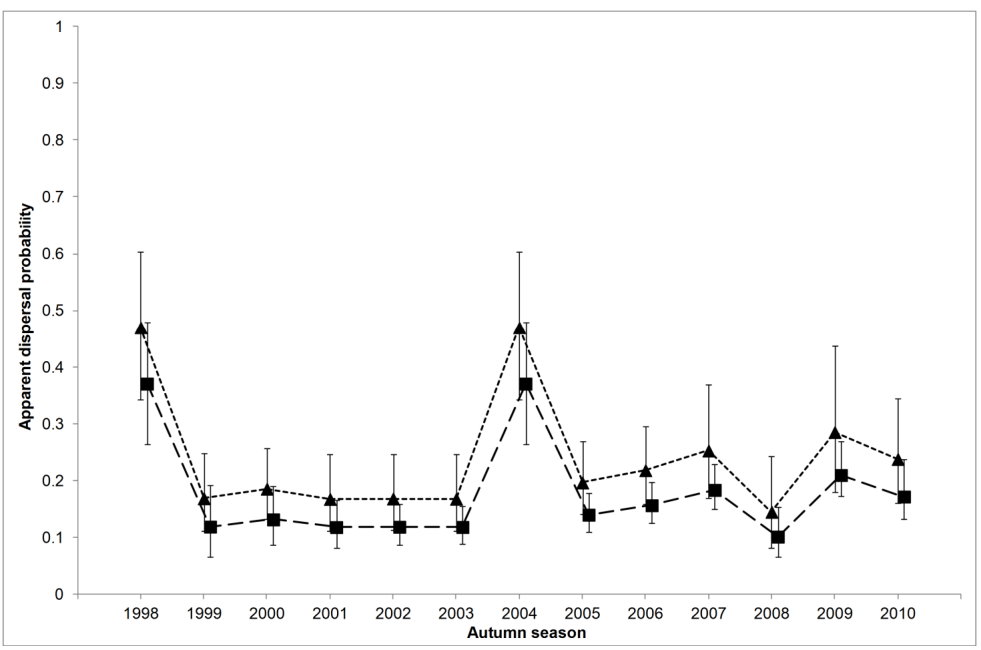

Figure S1. Apparent transience probability of Doñana-born glossy ibises resighted for the first time as juveniles (triangles, short-dashed line) and as adults (squares, long-dashed line). Estimates (95%CI) are from model 22 (Table S2).

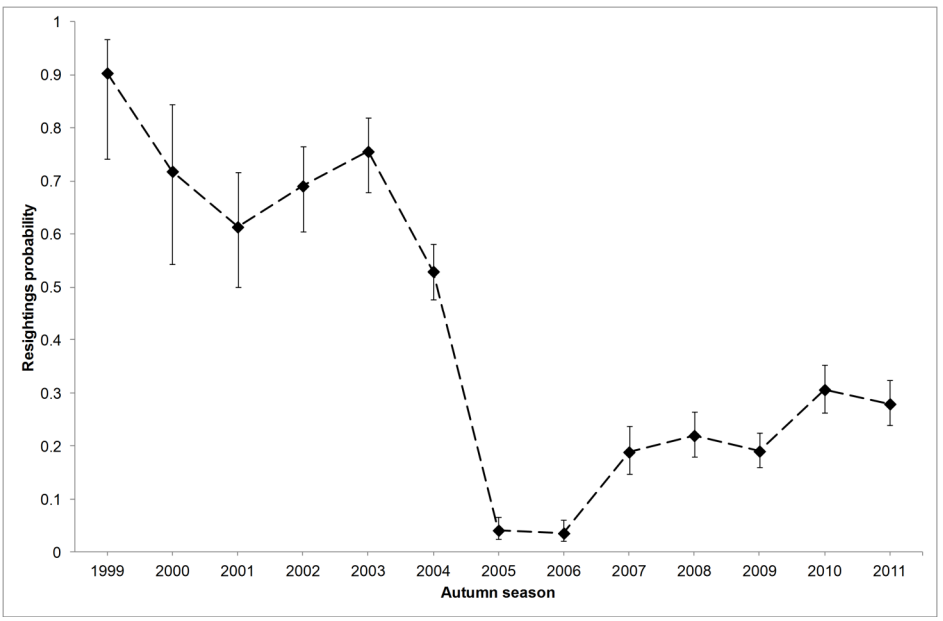

Figure S2. Probability of resighting at Doñana of native glossy ibises in autumn (October - December). Estimates (95%CI) are from the model with the lowest AICc (*bm2* in Table S1).

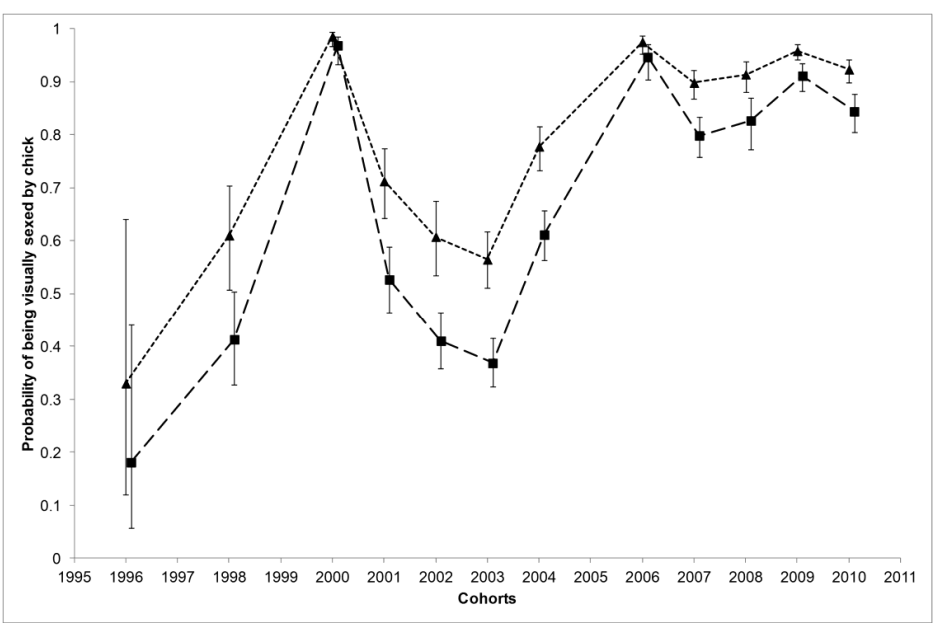

Figure S3. Probability for chicks of being visually sexed depending on birth year (best model for Visual Sexing, cfr Table S4 and Table S5). Females (short-dashed line) were more likely to be visually sexed than were males (long-dashed line). Estimates (95%CI) are from the model with the lowest AICc (22-2).

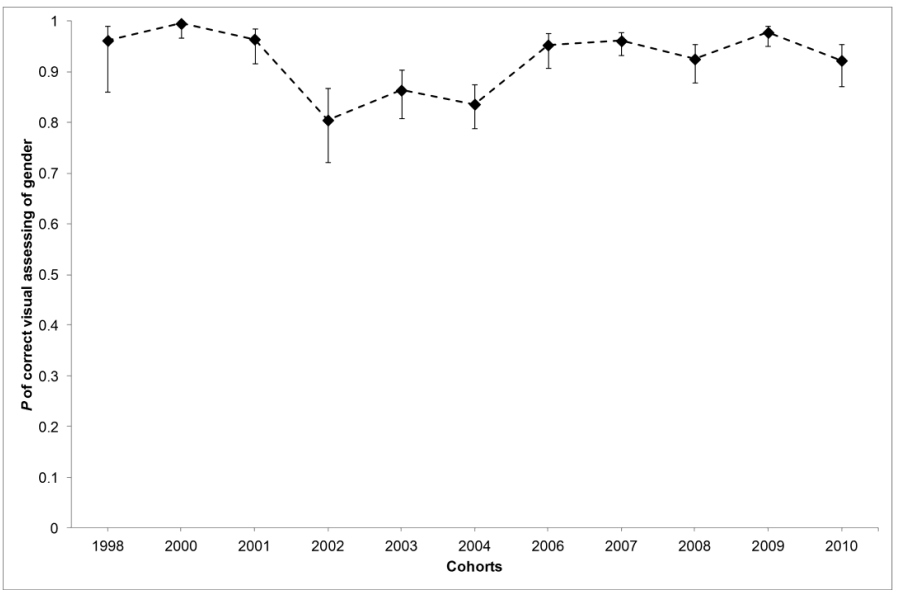

Figure S4. Probability for chicks of being correctly sexed visually in each year (best model for Correctness, cfr Table S4 and Table S5). Visual sexing was a quite reliable method but its reliability varied according to years. Estimates (95%CI) are from the model with the lowest AICc (22-2).

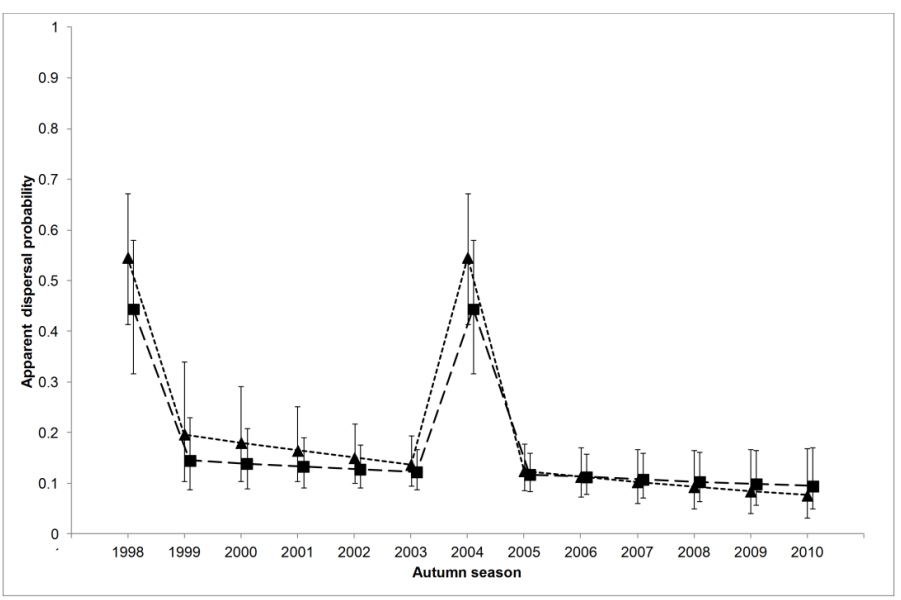

Figure S5. Residents' apparent dispersal probability of females (triangles, short-dashed line) and males (squares, long-dashed line). Estimates (95%CI) are from model 26 (Table S2).

Síntesis y Discusión General

En esta tesis doctoral se ha investigado la dinámica, desde sus comienzos, de una población de moritos, una especie de aves colonial que se había extinguido de nuestra área geográfica a lo largo del siglo pasado [1]. Para ello se han usado un conjunto de datos recolectados durante más de quince años que consisten de censos, sexados moleculares y visuales, seguimiento de individuos marcados y mediciones morfométricas (véase [2] para mayores detalles). Este sistema-modelo es particularmente interesante debido a que pocos estudios han investigado las dinámicas poblacionales de una especie a partir de sus comienzos, y la casi totalidad de ellos han sido sobre aves marinas existiendo entonces un cierto sesgo sistemático (véase [3–6]). Este tipo de investigaciones son cruciales para entender cómo los ciclos vitales varían según factores demográficos y ambientales y para predecir patrones de (re)distribución de las especies en respuesta al cambio global [7].

En esta memoria se ha demostrado que el asentamiento en Doñana ha sido favorecido por la creación y gestión de un espacio con condiciones idóneas para la cría de ésta y otras especies de aves (Capítulo I). Este primer resultado sugería que la dinámica poblacional en Doñana podría entenderse como parte integrante de una metapoblación cuyas poblaciones varían de tamaño e interactúan entre ellas siguiendo dinámicas complejas [8]. Dicha complejidad se ha reflejado por ejemplo en la variación temporal de la proporción de sexos, un importante parámetro demográfico, que ha sido modulado por un conjunto de respuestas adaptativas y no-adaptativas a cambios demográficos y ambientales (Capítulo II). También se ha señalado que el fuerte crecimiento poblacional ha sido alimentado en gran medida por el influjo de inmigrantes y que al mismo tiempo esta población ha representado una fuente para la dinámica metapoblacional abasteciendo a otras poblaciones con individuos nacidos en Doñana (Capítulo III). Finalmente, se ha confirmado el papel crucial que esta población ha tenido para la expansión de la

especie en la cuenca del Mediterráneo y Europa Occidental especialmente cuando sequías locales impidieron la cría de esta especie en Doñana; además de esto, se ha puesto en evidencia la existencia de dos clases de individuos en cuanto a hábitos dispersantes: por un lado (*i*) los residentes, más reacios a dispersar y en proporción creciente con el paso de los años, y por el otro (*ii*) los transeúntes cuya actitud a dispersar dependió al menos en parte del éxito reproductor de la colonia (Capítulo IV).

Capítulo I - Restauración de un humedal y colonización del morito

Se ha investigado el proceso de formación y crecimiento de la colonia mixta en el Lucio de la FAO que el morito colonizó después de haberse extinguido localmente entre finales del siglo XIX y comienzos del siglo XX. Aunque no existan datos ciertos sobre su distribución en tiempos históricos, algunos registros antiguos sitúan la presencia de esta especie como nidificante en el sur de la península Ibérica, concretamente en Doñana, a mediados del siglo XVIII [1]. Su declive a lo largo del siglo pasado podría haberse debido al impacto antrópico, particularmente al aumento de la actividad agrícola, la caza y la consecuente pérdida de humedales que acompañó el crecimiento económico en Europa a partir de comienzos del siglo XX [9]. De acuerdo con esta premisa, a lo largo del siglo pasado las poblaciones más importantes de moritos estaban todas en Europa del Este [10,11] donde el crecimiento económico y el consecuente impacto antrópico sobre los hábitats naturales no fue tan marcado [12]. Si la degradación y la fragmentación de los hábitats idóneos a su cría pudo ser la causa de su extinción local, no es de extrañar que la restauración de éstos fuera lo que favorecería su colonización.

De acuerdo con esta premisa, pocos años después de que se restaurara un espacio protegido con condiciones hídricas controladas

e ideales para la cría de ésta y otras especies afines, el morito volvió a criar en Doñana en 1996. Lo hizo con tan sólo siete parejas que colonizaron este nuevo espacio junto con la Garza Imperial (Ardea purpurea) y la Garcilla Cangrejera (Ardeola ralloides) a las cuales se fueron sumando con el paso del tiempo el Martinete (Nycticorax nycticorax), la Garceta (Egretta garzetta) y la Garcilla Bueyera (Bubulcus ibis). La restauración y gestión de esta zona se puede considerar un gran éxito del punto de vista ornitológico habiendo favorecido la colonización del morito y el crecimiento poblacional de ésta y otras especies de ardéidos (particularmente la garza imperial).

Los resultados obtenidos indican que el aumento de esta especie en este humedal no se debió a la simple redistribución de parejas dentro del área sino que fue un claro resultado del crecimiento de la población nidificante en Doñana. Algunos años después (en 2004) el morito empezó a criar también en otras áreas de Doñana, especialmente en sitios que, como el Lucio de la FAO, habían sido cercados para controlar la herbivoría y favorecer la regeneración de la vegetación.

Capítulo II – La proporción de sexos: causas no-adaptativas y adaptativas

Muy a menudo la proporción de sexos (SR de su acrónimo inglés) en especies monoicas es paritaria. A partir de esta premisa diversos científicos, entre ellos Darwin, sentaron las bases de lo que habría sido un campo muy activo de la biología evolutiva: la teoría de asignación por sexos (sex allocation theory). Las ideas que habían sido propuestas para explicar la alta frecuencia con la que machos y hembras se encontraban en la naturaleza con un ratio 1:1 fueron refinadas y esclarecidas por Fisher [13]. Éste tuvo el mérito de desviar la atención sobre el número de individuos de cada sexo para focalizarla sobre el gasto dedicado a producir descendientes de cada

uno de ellos; este cambio de enfoque ha tenido una repercusión muy importante en el desarrollo de otras teorías en este campo [14–16]. La idea general de Fisher es que, si hijos e hijas tienen el mismo éxito reproductor, los padres conviene invertirán lo mismo en cada sexo para maximizar su propia eficacia biológica (fitness) [16]. De hecho, si la cría de los hijos no es igual de costosa que la cría de las hijas, el SR esperado a nivel poblacional es sesgado hacia el sexo menos costoso (manteniendo la misma inversión en cada sexo) puesto que de hacer así se obtienen un número mayor de descendientes. A partir de este sencillo modelo de asignación por sexos se han considerado escenarios más complejos considerando escenarios alternativos a los supuestos por la hipótesis de Fisher. De hecho, cambios de SR pueden deberse a respuestas no-adaptativas (debido por ejemplo a tasas de mortalidad diversas por cada sexo [17]) o adaptativas como esperado según diversas otras teorías de asignación por sexo [14,16,18–20] que postulan el efecto de algún factor extrínseco (ambiental, demográfica, social, etc.) sobre el ratio costes/beneficios de machos y hembras. En aves la hipótesis de Fisher se ha testado sobre todo con especies de aves sexualmente dimórficas [21–23] asumiendo que el grado de dimorfismo refleje fielmente los costes de cría asociados a cada sexo. No obstante, este supuesto ha sido rara vez evaluado empíricamente [24].

En este estudio se ha calculado el coste metabólico de los pollos durante el crecimiento en relación al dimorfismo sexual en tamaño. Con estas estimas se ha calculado el SR esperado de acuerdo a los gastos energéticos estimados por cada sexo y asumiendo igual inversión por parte de los padres (hipótesis de Fisher). De acuerdo a los gastos energéticos calculados con el método del agua doblemente marcada [25], la proporción de sexos según Fisher resulta levemente sesgado hacia las hembras (0.465). Se estimó que la condición corporal media [26] de los pollos decayó de manera muy similar por cada sexo junto con el aumento del tamaño poblacional. Por otro

lado, se estimó indirectamente que al aumentar el tamaño poblacional aumentó la discrepancia entre la mortalidad de hembras y machos: aumentando desproporcionadamente la mortalidad de los pollos hembras en relación a la de los machos. Esto llevó a un SR de los volantones más sesgado hacia los machos a medida que aumentaba el tamaño de la colonia. También se encontró que el SR de los pollos más jóvenes (cercanos al nacimiento) siguió el patrón contrario y se ajustaron al SR esperado según Fisher. Curiosamente el SR de los volantones se correlacionó negativamente al SR poblacional en otoño tal como se estimó en el Capítulo III. El conjunto de estos resultados sugiere que al aumentar la competición y empeorar la condición corporal de los pollos de ambos sexos, las hembras al ser más pequeñas sufrieron una mayor mortalidad. Aunque se suele esperar el patrón contrario, es decir que el sexo más grande sufra una mayor mortalidad en condiciones de estrés [22,27–29], también puede darse el caso que los más grandes sean más capaces de aguantar condiciones críticas o que compitan por las cebas con el sexo más pequeño en una posición de ventaja debido a su mayor tamaño (por ej. [30]). El hecho de que la condición corporal decayera de manera parecida en cada sexo sugiere que este patrón no se debió a competición directa. Cualquiera que haya sido el proceso que ha llevado a una mayor mortalidad de las hembras, el exceso resultante de machos entre los volantones pudo ser contrarrestado por la simultánea creciente propensión a dispersar de éstos.

Este estudio sugiere que el SR de una especie puede cambiar de acuerdo a un complejo sistema de mecanismos adaptativos y no-adaptativos que hace particularmente difícil evaluar predicciones generales en especies, como las aves, con ciclos de vida complejos.

Capítulo III - Auto-reclutamiento, inmigración y papel de Doñana dentro de la metapoblacional del morito

Los procesos demográficos que subyacen a la distribución de las especies representan un tema central para la Ecología y cobran particular relevancia debido al cambio climático y otros impactos antrópicos. Sin embargo, para estudiar estos procesos en detalle, se requiere del uso de información recolectada a nivel de individuo, algo muy difícil de conseguir en la práctica. Las aves coloniales, por el hecho de concentrarse en los sitios de cría donde pueden ser más fácilmente monitoreadas, tienen un alto potencial para este tipo de investigaciones. De entre los pocos estudios que han descrito la dinámica de una población de aves desde su creación, muchos tienen como especie modelo aves coloniales marinas [3–6,31]. Por lo consiguiente, nuestros conocimientos de cómo ocurren estos procesos y de cuáles son los factores influyentes presentan un importante sesgo taxonómico. Uno de los aspectos más destacados en estos sistemas es el rol que el auto-reclutamiento y la inmigración pueden tener para el crecimiento de una nueva población. Varios trabajos parecen indicar que el rápido crecimiento de nuevas colonias podría sustentarse por el influjo de inmigrantes atraídos por una productividad mayor que en las colonias de origen [5,31]. Esto es coherente con la hipótesis de que el éxito reproductor de una colonia representa una información que los individuos son capaces de procesar y de usar para asentarse en un sitio o en otro [32,33]. Por otro lado, se ha postulado que el número de conspecíficos podría también interpretarse como un indicador del buen funcionamiento de la colonia y afectar la probabilidad que un individuo se establezca en una cierta área [34]. El tamaño poblacional también podría tener una relación negativa con la calidad de una colonia si a mayor densidad hay mayor competencia y entonces menos recursos disponibles.

Ninguna de estas hipótesis ha sido suportada por el análisis de la probabilidad de auto-reclutamiento en la colonia del Lucio de la FAO. No obstante, no se puede descartar que un efecto de denso-dependencia negativa se haya dado cuando la población de la FAO alcanzó las 700 parejas (en 2004) y se empezaron a diversificar los sitios de cría en Doñana. Esto es coherente con la reducción en las tasas de auto-reclutamiento en la FAO observadas para las cohortes sucesivas al 2003 que, posiblemente, tuvieron la posibilidad de dispersar a muy corta distancia a colonias con menor competencia y similares condiciones ambientales. Otro resultado a destacar es la temprana edad de primera reproducción: la probabilidad de auto-reclutamiento en la colonia fue la más alta (ap. 0.8) para individuos en su primer año de vida. Este, junto con el alto número de volantones por pareja, resultaron ser parámetros demográficos particularmente altos para la especie ([35–38] aunque véase [39] para las recientemente establecidas y muy productivas poblaciones argelinas). Aun así, se estimó que más de 60 hembras inmigrantes por año tuvieron que reclutar para que la población creciera tal como lo hizo. Aunque no resulte claro el origen de los colonizadores de Doñana así como de los inmigrantes que sostuvieron el crecimiento de esta población, es probable que las poblaciones de Éuropa del Este hayan jugado un papel importante. Mientras la población de Doñana estaba experimentando un crecimiento tan fuerte, las poblaciones del Éuropa Oriental, antaño las más importantes en esta región estaban sufriendo un declive [40]. Alrededor de tres de cada cuatro pollos anillados sobrevivieron y se quedaron en Doñana durante su primer año de vida, sin diferencias entre sexos. Aun así, la probabilidad de supervivencia local después del primer año de vida fue muy diferente entre sexos y estado reproductor. Los machos que habían reclutado al primer año de vida tuvieron probabilidades muy altas de sobrevivir y quedarse en la colonia: mucho más altas que aquellos que no habían reclutado. Las hembras que habían reclutado tuvieron

probabilidades de supervivencia local parecida a los individuos del primer año mientras que aquellos que no lo habían hecho tuvieron probabilidades algo más altas de sobrevivir y quedarse. Esto sugiere que mientras para los machos el no reclutar en el primer año de edad les empujaba a dispersar, para las hembras no fue así. Curiosamente, de acuerdo con el Capítulo II, la proporción de sexos con el paso del tiempo se sesgó hacia una mayoría de machos volantones que entonces tuvieron que sufrir una mayor competencia para encontrar pareja. Entonces, como se ha sugerido en esa misma sección, es verosímil que al aumentar la competencia entre los machos, estos fueron más propensos a dispersar si no pudieron reclutar en el primer año de vida. Finalmente, se puso de manifiesto que la población de la FAO y de Doñana en su conjunto representó una fuente de individuos para otras colonias que se fueron formando en la Cuenca del Mediterráneo y Europa Occidental.

En conclusión este estudio confirma para una especie de ave acuática la importancia de la inmigración para el rápido crecimiento de una nueva colonia de manera similar a los hallazgos hechos en aves marinas. Asimismo, se subraya la importancia de Doñana para la expansión y la conservación de esta especie. En términos generales, los resultados de este estudio sugieren que ya en etapas muy iniciales del proceso de formación y crecimiento de una colonia, ésta puede abastecer otras poblaciones con sus individuos y favorecer el proceso de expansión.

Capítulo IV – Las sequías locales como motor para la dispersión y expansión de la especie

La capacidad que las especies tienen de dispersar representa uno de los procesos de mayor importancia en Ecología. En particular, frente a los continuos cambios que los ecosistemas están actualmente sufriendo, la dispersión juega un papel fundamental para

la distribución, supervivencia y persistencia de las especies. En este contexto, el conocimiento de los mecanismos funcionales por los que se regula el proceso de dispersión asume una importancia vital para designar políticas de gestión adecuadas e intentar limitar los daños del cambio global sobre los ecosistemas [41]. La propensión a dispersar de un individuo puede depender de factores intrínsecos como el sexo [42], la edad [43], la condición física [44] o la personalidad [45,46] que pueden interactuar más o menos directamente con factores extrínsecos como son las condiciones ambientales y demográficas [47]. Recientemente se ha enfatizado la necesidad de estudiar cómo el cambios climático y en particular los eventos climáticos extremos (que se prevé aumenten de intensidad y frecuencia; [48]) pueden afectar a la propensión a dispersar [7]. De los pocos estudios que han estudiado el impacto de los eventos climáticos extremos sobre los parámetros demográficos [7,49], muy pocos se han focalizado sobre la dispersión [50].

En este estudio se ha analizado el efecto de factores intrínsecos y extrínsecos, entre ellos las sequías locales, sobre la propensión de los moritos nacidos en Doñana a dispersar (sensu emigración). No se han encontrado evidencias de diferencias entre sexos ni grupos de edad (primer año y resto) así como efectos de recursos tróficos disponibles o de denso-dependencia. Debido a que el parámetro de interés que se usó para validar la hipótesis sobre la propensión a dispersar depende también de la tasa de mortalidad (se habla de hecho de "dispersión aparente"), no se dispone de estimas absolutas de la probabilidad de dispersión. Sin embargo, se ha visto que en el caso de las sequías en Doñana la tasa de dispersión aparente aumentó por aproximadamente dos veces y media con respecto al resto de años. Datos de reavistamientos de individuos de Doñana en Marruecos y en otras regiones del Mediterráneo y Europa confirmaron que a partir de la última sequía (en 2005) hubo un aumento de individuos que dispersaron de Doñana. Como mencionado en la

sección anterior, el éxito reproductor proprio o de los conspecíficos puede representar una información útil para decidir si reclutar en una colonia o dispersar [32,33,51]. Por lo tanto, es probable que la mayor tasa de dispersión en años de sequía se pueda explicar por la falta de reproducción asociada a estos eventos. El efecto de la sequía sobre la dispersión fue muy similar para dos grupos de individuos que se establecieron según la mayor o menor frecuentación que habían tenido del área: los residentes y los transeúntes. Por otro lado, en años normales (húmedos) hubo una tendencia al aumento de la proporción de residentes junto con el aumento del tamaño poblacional, mientras que para los transeúntes la tendencia en dispersar estuvo negativamente correlacionada a la productividad de la colonia. Al menos dos hipótesis pueden explicar el progresivo aumento de la proporción de residentes a lo largo de los años: (i) la creciente experiencia acumulada hizo cada vez menos conveniente dispersar (como demostrado en [52,53]), o (ii) de acuerdo al tiempo pasado desde el asentamiento de una colonia (y entonces a su rol en el proceso de expansión) pudo haber predominado un fenotipo más dispersante antes y más filopátricos después (véase por ej. [54]). Finalmente, la razón de sexos en la población invernante sugirió que con el paso del tiempo y el crecimiento de la población se pasó de una mayoría de machos a una ligera mayoría de hembras. Si, como sugerido en el Capítulo II, la tasa de dispersión dependió de la interacción entre el efecto del sexo y de la densidad con los machos progresivamente más inclines a dispersar, eso explicaría por qué no se ha encontrado un efecto directo del sexo sobre la dispersión aparente puesto que, debido a criterios de parsimonia, no se pudo testar un modelo para tales efectos. De una análoga manera se podría explicar la falta de apoyo para un efecto de denso-dependencia: si tal efecto difiriera entre individuos con diferentes características (véase por ejemplo cuánto sugerido anteriormente con relación al sexo), el tipo de modelos usados no habría permitido

detectarlo. Alternativamente, este resultado podría también explicarse si el tamaño poblacional no hubiera alcanzado un cierto umbral por debajo del cual los efectos de denso-dependencia no son apreciables [55]. En general, en aves los juveniles suelen tener mayor propensión a dispersar que los adultos [56]; el hecho de que no se encontrara tal efecto pudo deberse a falta de poder estadístico debido también a los modelos que sólo permitían analizar el efecto edad entre los transeúntes (y no entre los residentes que por definición eran todos mayores de un año de edad). Aparentemente, los individuos con experiencia previa de cría son más reacios en abandonar el área mientras que los otros son más proclives a abandonar el área en el caso de que el éxito reproductor no sea bueno. Este patrón es coherente con la idea de que individuos con experiencia previa de cría sean mejores reproductores [57] y que entonces tengan más que perder (como potencial reproductor) frente a los riesgos relacionados a la dispersión. También es razonable pensar que individuos con escasa experiencia previa confíen más en la experiencia colectiva de cuánto hagan individuos expertos.

Finalmente, el interés mayor de este estudio deriva de los resultados que aportan evidencia sobre cómo los eventos climáticos extremos pueden propulsar la dispersión y la expansión de una especie (véase también [50]).

Futuras líneas de trabajo

En esta tesis doctoral se ha explorado la dinámica poblacional de una especie en expansión a través de una nueva población en pleno crecimiento demográfico. En particular se han presentado resultados relevantes sobre los parámetros demográficos más importantes para el crecimiento poblacional, de los factores intrínsecos y extrínsecos que favorecen la dispersión y la expansión de una especie y, finalmente, de la compleja red de mecanismos adaptativos y no adaptativos que modulan la proporción de sexos a

nivel poblacional. También se ha contribuido a través del uso de modelos de proyección poblacional a esclarecer parcialmente el papel fuente/sumidero que esta población puede haber tenido a nivel metapoblacional.

No obstante, una deseable línea de investigación a abrir en futuro sería investigar su dinámica metapoblacional a través del uso de datos de individuos marcados recolectados a lo largo de estos años sobre todo en el área del Mediterráneo y en Europa. La existencia de programas de marcaje individual en varias colonias que han ido surgiendo en estos últimos años es esperanzadora frente a esta perspectiva. En los últimos años se están afirmando nuevas metodologías, muchas de ellas basadas en aproches de tipo Bayesiano, como por ejemplo los "Integrated Population Models" [58] y otros modelos parecidos pero con una componente espacial explicita [59] que podrían resultar particularmente idóneos para modelar estos datos. De esta manera, se podrían obtener estimas independientes de supervivencia y dispersión así como analizar hipótesis ecológicas sobre la dinámica metapoblacional de una manera mucho más contundente a cuanto se ha hecho en esta tesis.

Para aportar un mayor grado de detalle sobre la dinámica metapoblacional sería deseable acoplar al estudio demográfico un estudio genético que permita esclarecer el flujo génico entre diferentes poblaciones de moritos. En este contexto, resulta particularmente sugerente el hallazgo de varios individuos marcados en Doñana en Centro América. Se ha sugerido de hecho que la colonización del morito en América haya ocurrido a través de la llegada de individuos desde Europa [60] pero actualmente no existen pruebas directas de ello.

Otra línea de investigación futura a tener en cuenta es el estudio de la componente espacial de la dispersión del morito, en particular de la distancia de dispersión. Más allá de cuanto investigado en esta tesis a propósito de la propensión a dispersar,

sería interesante investigar si diferentes clases de edad y sexo tienen un patrón de dispersión que difiere en su componente espacial. Este objetivo ya está al alcance puesto que existe una gran cantidad de datos de reavistamiento y recuperación de individuos marcados en Doñana.

Los resultados a nivel de Doñana sugieren que hay variación en la razón de sexos con un progresivo aumento de los machos entre los volantones. Este exceso de machos parece haber sido contrarrestado por una simultanea mayor propensión a dispersar de éstos. No obstante, no conocemos que está ocurriendo en las otras poblaciones conectadas a Doñana en cuanto a razón de sexos. Sería interesante investigar cómo la proporción de sexos varía no sólo entre diversas clases de edad sino también entre diversas poblaciones de una metapoblación. Esto contribuiría mucho a nuestros actuales conocimientos sobre la teoría de asignación por sexo aplicada a aquellos grupos taxonómicos con estrategias vitales más complejas como son los vertebrados.

Uno de los resultados relevantes de esta tesis doctoral es el hecho de haber descrito dos grupos de individuos en cuanto a hábitos dispersantes. Por un lado aquellos individuos con una tendencia más filopátrica, que con el paso de los años han ido aumentando como proporción. Por el otro aquellos más propensos a dispersar aparentemente afectados por el éxito reproductor de la colonia. No parece que esta diferencia pudiera explicarse simplemente por diferencia de clase de edad. En los últimos años se ha sugerido que este tipo de procesos podrían tener una base genética (personalidad; [45,61,62]) e incluso relacionarse a la "edad" de la colonia y al proceso de expansión de una especie [46,54]. Para ampliar el conocimiento sobre los procesos que regulan la distribución de las especies se necesitan más estudios sobre este tema usando diversas especies con estrategias vitales diferentes.

Conclusiones

A continuación se detallan los resultados principales obtenidos en este tesis doctoral:

1. La restauración de un humedal a régimen semi-artificial dentro del Espacio Natural de Doñana ha favorecido el asentamiento y el crecimiento de una población de morito que había desaparecido de Europa Occidental desde hace al menos un siglo. Esta actuación ambiental ha sido también muy importante para la dinámica poblacional de varias especies de ardeidos, en particular para la Garza imperial.

2. La población de moritos en Doñana ha sido clave para la expansión de la especie en el área Mediterránea y Europea.

3. El fuerte crecimiento poblacional en los primeros años se debió en gran medida al influjo de inmigrantes. En particular, es probable que el origen de estos inmigrantes sea a partir de poblaciones de Europa del Este que han sufrido un declive poblacional en los últimos años.

4. Aun situándose en el margen de su área de distribución y en pleno crecimiento poblacional gracias a la llegada de inmigrantes, la población de Doñana ha sido, desde una óptica metapoblacional, una población fuente que ha suministrado emigrantes hacia otras colonias de reciente aparición en Éuropa occidental y en el área del Mediterráneo.

5. Como es de esperar en una población nueva con niveles de competición intraspecíficos aun modestos, los parámetros demográficos intrínsecos (productividad, edad de primera reproducción y supervivencia) se ajustan a aquellos esperados para una especie en crecimiento y en general parecen mejores frente a aquello descritos en literatura para poblaciones más estables.

6. Los eventos climáticos extremos como son las sequías en Doñana producen un importante aumento en la tasa de dispersión.

7. Grupos de individuos con características diversas pueden tener relaciones muy diferentes entre la propensión a dispersar y las condiciones ambientales.

8. La tasa de mortalidad de los pollos hembras ha aumentado en relación a la de los pollos machos a medida que aumentaba la población. Es probable que esto se relacione al menor tamaño de las hembras que les hace más vulnerables a malas condiciones ambientales. Como consecuencia de ello, al aumentar la densidad y supuestamente la competición se encuentra una progresivamente mayor prevalencia de machos entre los volantones. Este exceso de machos parece ser contrarrestado por el simultáneo aumento de la probabilidad de dispersión de este sexo.

9. La razón de sexos al nacimiento así como descrita por los pollos más jóvenes se sesga hacia las hembras al aumentar la densidad siguiendo el patrón contrario a la razón de sexos de los volantones. Posiblemente, esto podría haberse debido a una respuesta adaptativa a la mayor prevalencia de machos debida a la mayor mortalidad de las hembras. Las hembras costarían menos que los machos debido a que por su mayor mortalidad tienen un periodo de cría más corto y al mismo tiempo serían una mejor inversión debido a que son más escasas numéricamente que los machos.

10. La proporción de sexos ha variado de manera distinta entre varias clases de edad (nacimiento, volantones, adultos) según respuestas adaptativas y no adaptativas. Este resultado pone de manifiesto la necesidad de considerar la complejidad de la estrategia vital de los vertebrados para los cuales los modelos teóricos clásicos de asignación por sexo pueden ser inadecuados.

Bibliografía

1. Figuerola J, Mañez M, Ibáñez F, García L, Garrido H (2004) Morito común Plegadis falcinellus. Libro rojo de las Aves de España. Dirección general para la Biodiversidad. Madrid: SEO/BirdLife. pp. 74–76. Available: http://www.xoriguer.org/ftpdescarregues/libro_rojo_aves_espana.pdf#page=74. Accessed 22 August 2012.

2. Mañez M, Rendón-Martos M (2009) El morito común , la espátula común y el flamenco común en España . Población en 2007 y método de censo. Máñez M, Rendón-Martos M, editors Madrid: SEO/Birdlife.

3. Porter J, Coulson J (1987) Long-term Changes in Recruitment to the Breeding Group, and the Quality of Recruits at a Kittiwake Rissa tridactyla colony. J Anim Ecol 56: 675–689.

4. Oro D, Ruxton GD (2001) The formation and growth of seabird colonies: Audouin's gull as a case study. J Anim Ecol 70: 527–535.

5. Kildaw S, Irons D, Nysewander D, Buck C (2005) Formation and growth of new seabird colonies: the significance of habitat quality. Mar Ornithol 58: 49–58.

6. Tims J, Nisbet I, Friar M, Mostello C, Hatch J (2004) Characteristics and Performance of Common Terns in Old and Newly-established Colonies. Waterbirds 27: 321–332.

7. Jenouvrier S (2013) Impacts of climate change on avian populations. Glob Chang Biol: 1–22. Available: http://doi.wiley.com/10.1111/gcb.12195. Accessed 16 March 2013.

8. Hanski I (1998) Metapopulation dynamics. Nature 396: 41–49.

9. Finlayson C, Davidson N (1999) Global review of wetland resources and priorities for wetland inventory. Preface IV Summary Report.

10. Cramp S, Simmons KEL (1977) Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic. Vol. I: Ostrich to ducks. Oxford: Oxford University Press. Available: http://scholar.google.es/scholar?q=Handbook+of+the+Birds+of+Europe,+the+Middle+East+and+North+Africa.+volume+1&btnG=&hl=es&as_sdt=0#1. Accessed 29 August 2012.

11. Del Hoyo J, Elliott A, Sargatal J, Cabot J, Jutglar F (1992) Handbook of the birds of the world: IBIS and SPOONBILLS.

12. De Vries B, Goudsblom J (2004) Mappae mundi: humans and their habitats in a long-term socio-ecological perspective: myths, maps and models. Amsterdam University Press.

13. Fisher RA (1930) The Genetical Theory of Natural Selection. Oxford,UK:Clarendon: Dover.

14. Charnov EL (1982) The Theory of Sex Allocation. Princeton University Press.

15. Hardy ICW, Cockburn A, Legge S, Double MC (2002) Sex ratios: concepts and research methods. Cambridge Univ Pr.

16. West SA (2009) Sex allocation. Princeton Univ Pr.

17. Leigh EGJ (1970) Sex Ratio and Differential Mortality between the Sexes. Am Nat 104: 205–210.

18. Trivers RL, Willard DE (1973) Natural Selection of Parental Ability to Vary the Sex Ratio of Offspring. 179: 90–92.

19. Hamilton WD (1967) Extraordinary sex ratios. Science (80-) 156: 477–488.

20. Wild G, West SA (2007) A sex allocation theory for vertebrates: combining local resource competition and condition-dependent allocation. Am Nat 170: E112–28. Available: http://www.ncbi.nlm.nih.gov/pubmed/17926288. Accessed 31 January 2014.

21. Stamps JA (1990) When Should Avian Parents Differentially Provision Sons and Daughters ? Am Nat 135: 671–685.

22. Anderson DJ, Budde C, Apanius V, Martinez Gomez JE, Bird DM, et al. (1993) Prey Size Influences Female Competitive Dominance in Nestling American Kestrels (Falco sparverius). Ecology 74: 367–376.
23. Torres R, Drummond H (1999) Does large size make daughters of the blue-footed booby more expensive than sons? J Anim Ecol 68: 1133–1141.
24. Magrath MJL, Van Lieshout E, Pen I, Visser GH, Komdeur J (2007) Estimating expenditure on male and female offspring in a sexually size-dimorphic bird: a comparison of different methods. J Anim Ecol 76: 1169–1180.
25. Speakman JR (1998) The history and theory of the doubly labeled water technique. Am J Clin Nutr 68: 932S–8S.
26. Peig J, Green AJ (2009) New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. OIKOS 118: 1883–1891.
27. Clutton-Brock TH, Albon SD, Guinness FE (1985) Parental investment and sex differences in juvenile mortality in birds and mammals. Nature: 131–133. Available: http://www.nature.com/nature/journal/v313/n5998/abs/313131a0.html. Accessed 3 February 2014.
28. Arroyo BE (2002) Fledgling sex ratio variation and future reproduction probability in Montagu's harrier, Circus pygargus. Behav Ecol Sociobiol 52: 109–116. Available: http://link.springer.com/10.1007/s00265-002-0496-9. Accessed 5 February 2014.
29. Bortolotti GR (1986) Influence of Sibling Competition on Nestling Sex Ratios of Sexually Dimorphic Birds. Am Nat 127: 495–507.
30. Adams EM, Frederick PC (2009) Sex-Related Mortality of White Ibis (Eudocimus albus) Nestlings During a Starvation Event. Waterbirds 32: 123–127.

31. Martínez-Abraín A, Oro D, Jimenez J (2001) The dynamics of a colonization event in the european shag: the roled of immigration and demographic stochasticity. Waterbirds 24: 97–102.

32. Danchin E, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79: 2415–2428.

33. Boulinier T, Danchin E (1997) The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. Evol Ecol 11: 505–517.

34. Stamps J (1988) Conspecific Attraction and Aggregation in Territorial Species. Am Nat 131: 329–347.

35. Lowe KW (1983) Egg size, clutch size and breeding success of the Glossy Ibis Plegadis falcinellus. Emu 83: 31–34.

36. Miller L, Burger J (1978) Factors affecting nesting success of the glossy ibis. Auk 95: 353–361.

37. Burger J (1978) Competition between cattle egrets and native North American herons, egrets, and ibises. Condor 80: 15–23.

38. Williams B (1975) Growth rate and nesting aspects for the Glossy Ibis in Virginia. Raven 46: 35–51.

39. Boucheker A, Nedjah R, Samraoui F, Menaï R, Samraoui B (2009) Aspects of the Breeding Ecology and Conservation of the Glossy Ibis in Algeria. Waterbirds 32: 345–351. Available: http://www.bioone.org/doi/abs/10.1675/063.032.0215. Accessed 9 December 2012.

40. Burfield I, van Bommell F (2004) Birds in Europe: Population Estimates, Trends, and Conservation Status. Cambridge (UK): BirdLife International.

41. Travis JMJ, Dytham C (2012) Dispersal and climate change: a review of theory. In: Clobert J, Baguette M, Benton TG, Bullock JM, editors. Dispersal Ecology and Evolution. Oxford University Press. pp. 337–348. Available: http://books.google.es/books?hl=es&lr=&id=wC9qnr4dH5AC&oi=fnd

&pg=PA337&dq=dispersal+and+climate+change+a+review+of+theory&ots=o1vKbP7rFc&sig=0lO4T7N_RwBqFz16AoNPlJ0ujpk. Accessed 12 December 2012.

42. Gowaty PA (1993) Differential Dispersal, Local Resource Competition, and Sex Ratio Variation in Birds. Am Nat 141: 263–280.

43. Kentie R, Both C, Hooijmeijer J, Piersma T (2014) Age-dependent dispersal and habitat choice in black-tailed godwits Limosa limosa limosa across a mosaic of traditional and modern grassland habitats. J Avian Biol 45: 396–405. Available: http://doi.wiley.com/10.1111/jav.00273. Accessed 6 October 2014.

44. Barbraud C, Johnson AR, Bertault G (2003) Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition. J Anim Ecol 72: 246–257. Available: http://doi.wiley.com/10.1046/j.1365-2656.2003.00695.x.

45. Cote J, Clobert J, Brodin T, Fogarty S, Sih A (2010) Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. Philos Trans R Soc Lond B Biol Sci 365: 4065–4076. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2992741&tool=pmcentrez&rendertype=abstract. Accessed 28 February 2013.

46. Duckworth RA, Badyaev A V (2007) Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proc Natl Acad Sci U S A 104: 15017–15022. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1986605&tool=pmcentrez&rendertype=abstract.

47. Matthysen E (2012) Multicausality of dispersal: a review. In: Clobert J, Baguette M, Benton TG, Bullock JM, editors. Dispersal Ecology and Evolution. Oxford University Press. pp. 3–18. Available: http://books.google.es/books?hl=es&lr=&id=wC9qnr4dH5AC&oi=fnd&pg=PA3&dq=dispersal+ecology+and+evolution+autor:matthysen&o

ts=o1vK8R4qFb&sig=cASjiEkoCWtoafZl6NOY50vKlY0. Accessed 9 December 2012.

48. Easterling D, Evans J, Groisman Py, Karl T, Kunkel K, et al. (2000) Observed Variability and Trends in Extreme Climate Events : A Brief Review. Bullettin Am Meteorol Soc 81: 417–425.

49. Moreno J, Møller AP (2011) Extreme climatic events in relation to global change and their impact on life histories. Curr Zool 57: 375–389.

50. Dugger KM, Ainley DG, Lyver PO, Barton K, Ballard G (2010) Survival differences and the effect of environmental instability on breeding dispersal in an Adelie penguin meta-population. Proc Natl Acad Sci 107: 12375–12380. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2901434&tool=pmcentrez&rendertype=abstract. Accessed 18 March 2013.

51. Brown CR, Brown MB, Danchin E (2000) Breeding habitat selection in cliff swallows: the effect of conspecific reproductive success on colony choice. J Anim Ecol 69: 133–142.

52. Balkiz Ö, Béchet A, Rouan L, Choquet R, Germain C, et al. (2010) Experience dependent natal philopatry of breeding greater flamingos. J Anim Ecol 79: 1045–1056.

53. Serrano D, Tella JL, Forero MG, Donázar JA (2001) Factors affecting breeding dispersal in the facultatively colonial lesser kestrel : individual experience vs. conspecific cues. J Anim Ecol 70: 568–578.

54. Duckworth RA (2008) Adaptive dispersal strategies and the dynamics of a range expansion. Am Nat 172 Suppl : S4–17. Available: http://www.ncbi.nlm.nih.gov/pubmed/18554143. Accessed 14 March 2013.

55. Matthysen E (2005) Density-dependent dispersal in birds and mammals. Ecography (Cop) 28: 403–416.

56. Switzer P V (1993) Site fidelity in predictable and unpredictable habitats. Evol Ecol 7: 533–555. Available:

http://www.springerlink.com/content/g5h624m730762894/. Accessed 20 November 2011.

57. Desprez M, Pradel R, Cam E, Monnat J-Y, Gimenez O (2011) Now you see him, now you don't: experience, not age, is related to reproduction in kittiwakes. Proc Biol Sci 278: 3060–3066. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3158944&tool=pmcentrez&rendertype=abstract. Accessed 30 January 2013.

58. Besbeas P, Freeman S, Morgan B (2005) The potential of Integrated Population Modelling. Aust N Z J Stat 47: 35–48.

59. Chandler RB, Clark JD (2014) Spatially explicit integrated population models. Methods Ecol Evol: 1–10. Available: http://doi.wiley.com/10.1111/2041-210X.12153. Accessed 24 July 2014.

60. Patten MA, Lasley GW (2000) Range Expansion of the Glossy Ibis in North America. North Am birds 54: 241–247.

61. Mueller JC, Edelaar P, Carrete M, Serrano D, Potti J, et al. (2014) Behaviour-related DRD4 polymorphisms in invasive bird populations. Mol Ecol 23: 2876–2885. Available: http://www.ncbi.nlm.nih.gov/pubmed/24750181. Accessed 3 October 2014.

62. Fogarty S, Cote J, Sih A (2011) Social personality polymorphism and the spread of invasive species: a model. Am Nat 177: 273–287. Available: http://www.ncbi.nlm.nih.gov/pubmed/21460537. Accessed 9 October 2014.

Agradecimientos

En lo más laboral, mis agradecimientos van primero a mis dos directores de tesis: Jordi y Andy. Muchas gracias a los dos por haberme dado la oportunidad de empezarme en el menester de la investigación: era lo que soñaba hacer y después de estos años tengo aun más entusiasmo que antes. Cada uno me habéis aportado un enfoque personal sobre cómo se investiga pero lo que desde mi punto de vista es el mensaje principal que me llevo de vosotros son dos conceptos: el pragmatismo y la síntesis, dos reglas esenciales para ser investigador. No basta la curiosidad, que de esa no faltaba ni siquiera antes. Sobretodo a la hora de escribir, no es fácil dejar de lado la retórica para dar prioridad a la sustancia, pero si hoy en día lo hago un poco mejor que hace unos años también os lo debo a vosotros.

Gracias también al Equipo de Seguimiento de Procesos Naturales de la EBD, en particular a Manolo Mañez y a Luis García, sin vuestro esfuerzo y profesionalidad no habría tenido la posibilidad de hacer esta Tesis. También gracias a Giacomo Tavecchia, Arnaud Bechet y Juan Amat por participar en mi Comité de Tesis y haberme echado una mano en muchas ocasiones. En la parte de captura-recaptura también me habéis echado un cable muy importante Ana Sanz-Aguilar y Roger Pradel. Gracias a Laura Serrano, mi tutora en la Universidad de Sevilla, por tu gran disponibilidad.

Viniendo a la parte más personal de lo que han sido estos años de Tesis se me ocurre que lo que más le falta a uno es el tiempo. Tiempo para hacer las cosas cómo te gustaría hacerlas. Sobretodo tiempo para aprender, aprender de todo que para eso estamos al mundo, aprender de modelos de dinámica poblacional, de life-history, de mates, de cine, de literatura, de historia, de música, de cómo abrir un huevo duro soplando en la cáscara, de todo vamos. De esta

reflexión surgen mis agradecimientos a Alex (que no se te suba a la cabeza, es por exigencia del guión que te nombro antes) por regalarme el libro sobre la Cultura (toda) que de todas maneras aun no he tenido tiempo de leer (por cierto si encuentras el libro sobre la Ciencia – toda – avísame). Y es que seguramente de tener más tiempo echaría uno en falta tener aun más, así que me conformo con el que tengo y a tirar pa 'lante. Por ejemplo no voy a tener mucho tiempo para escribir estos agradecimientos así que pido perdón a cualquiera se pueda sentir indignamente representado en estas líneas: es por falta de tiempo, no es otra cosa. Desde que he empezado la Tesis han pasado varios años pero sobre todo han pasado un montón de cosas. Hubo un tiempo, al comienzo, en el que aquello fue la japi-pandi. Fue el tiempo 'sinceritá', 'mambo italiano', alfalfa, alameda y fiesta-fiesta. Muy divertido. Gracias también a todos aquellos que aunque no mencione aquí explícitamente formaron parte de la japi-pandi en un momento u otro. Luego hubo un tiempo de organizarse para el futuro, coche, casa, mudanzas. Mucha ilusión. Por cierto gracias Grego también por haberte dejado enredar en aquella mudanza extrema – todo un detalle. Y luego vino el tiempo de empezar a recoger lo que uno había ido sembrando, por ejemplo hijos. Mucha revolución y en eso estamos.

Dando un paso atrás, me acuerdo perfectamente del momento en que supe que me habían concedido la beca JAE, del vértigo de alegría y esa sensación de puertas que se abrían. Doy las gracias a Andrea por haber compartido al 100% conmigo ese momento y esa ilusión. A ella le doy muchas gracias por un montón de cosas que no voy a decir aquí y por otras que sí puedo decir sin resultarle meloso al desaventurado que tiene este librecito entre sus manos con la idea de leer sobre dinámica poblacional en aves y no sobre declaraciones de amor entre humanos. Ah! muchas gracias por haber elegido un trabajo que además de ser bonito, como lo hice yo, también te permite dar de comer a nosotros y a la progenie, Fabio y Ainara, a los

que doy las gracias por haberme abierto las puertas a una etapa completamente nueva de mi vida. No cabe duda que sois los niños más bonitos del mundo mundial así que gracias por ello (vale que es un tanto empalagoso pero algo biológico-visceral me empuja a ello, iperdón!). Quedándome en lo familiar muchas gracias a los abuelos que, mi caso lo demuestra una vez más, sois la generación fundamental para que el país siga de pié (pero también los tíos/as no son para menos, ¿eh?). Sin vuestra ayuda habría tenido bastante menos tiempo para dedicarle a esto. Rimanendo in ambito famigliare ringrazio ai miei vecchi amici per continuare ad esserlo dopo anni di assenza dal suolo patrìo. siete pochi, vi chiamate quasi tutti uguale, ma siete buoni amici: Andrea, Andrea, Andrea, Max (personal communication) e Valentina.

En cuanto a lo que ha sido mi doctorado, además de las personas que he mencionado antes, también le tengo que dar las gracias a unos cuantos fórums en internet. De esos fórums he sido y sigo siendo frecuentador constante, ahí me encuentro con un montón de gente a la que no conozco y que no me conoce pero que me han ayudado y me ayudan a aprender cosas. Cosas muy importantes para mi tesis y para mi formación.

Luego es que trabajo y amistad a menudo se mezclan y uno se encuentra a hablar, y mucho, de trabajo con compañeros que pronto llegan a ser amigos. Como en quizás todas las cosas los extremos no convienen así que no hay nada malo en hablar de trabajo con los amigos pero no hay nada bueno en hablar exclusivamente de trabajo con los amigos. Esta circunstancia no se ha dado con ninguno de ellos, gracias por ello. Así que: gracias a Letizia por tu sabiduría y serenidad 'frosinate' que siempre me dan un punto de vista diferente sobre las cosas; a Chiara por las charlas apasionadas y por tu visión 'montanara' del mundo; a Zulima por tu tremendo sentido crítico, humor caustico y por apreciar tanto mi camiseta-pera; a Irene por esa mezcla de entusiasmo, ironía y afán existencial que uno nunca se

aburre contigo; a Massimo por cómo cuentas las cosas y por ser aquel bailarín inolvidable que los que estaban en mi boda aun se acuerdan todos de ti; a Alessandro por ser tan buen compañero de charlas y por compartir conmigo el sentido del humor y de la humildad; a Giulia por tu cercanía y por ser de aquellas personas que en un momento dado he conocido y es como si ya te conocía de antes; a Cristina por darme la lata, por dejarte dar la lata y por tus imprevisibles y geniales nexos lógicos; a Marcello para tu optimismo cósmico y para tu absoluto mal gusto en materia de cine que me permite dar libre desahogo a mis instintos cinéfilos más abyectos; a Raquel, por, entre otras cosas, tener buen gusto en materia de cine y entonces ayudarme contra mis instintos cinéfilos más abyectos; a Christophe por haberme hecho reír en cuanto pisaste tierra sevillana; a Duarte por ser tan luso y muy buen compañero de Tesis; a Javier de manera particular por haberme enseñado tu Fuenteheridos más espectacular; a Carlos R. por tener esas ganas de hacer tan pegadizas; y luego a muchos otros con los que lo he pasado, y sigo haciéndolo, muy bien: Rocío, Laura, Mónica, Marga, Peter, Cristina P., Anna, Camille, Carlos M, Quini, Josué, Rafa, Juanele, Vanessa, Roger, Ainara y muchos otros.

Finalmente muchas gracias a los moritos por haberos dejado estudiar todos estos años (no teníais más remedio – pero os lo agradezco de todas maneras).